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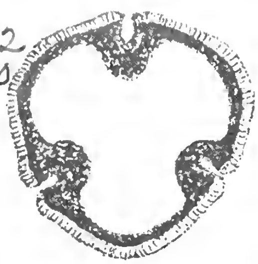
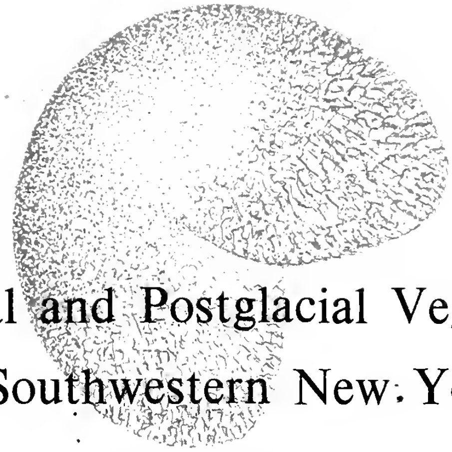
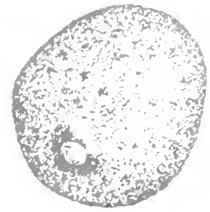
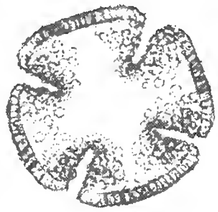
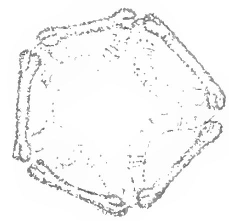
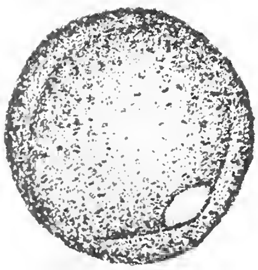




Late-glacial and Postglacial Vegetation Change in Southwestern New York State


Norton G. Miller
Temporary Botanist, Biological Survey

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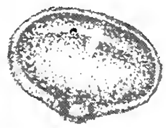
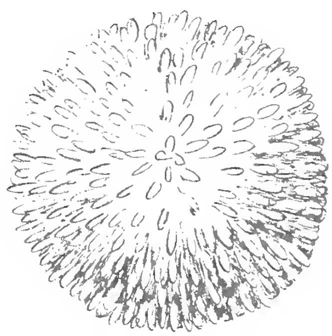

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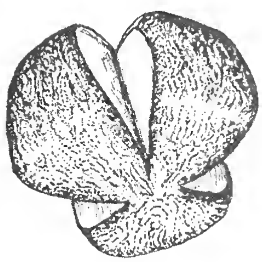
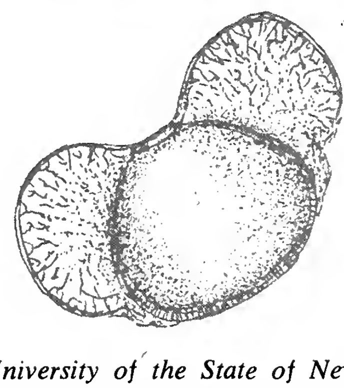

The University of the State of New York
The State Education Department/Albany, New York/April 1973

Late-glacial and Postglacial Vegetation Change in Southwestern New York State

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Bulletin 420
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Late-glacial and Postglacial Vegetation Change in Southwestern New York State [1, 2]

Norton G. Miller [3]

ABSTRACT

Pollen stratigraphy in sediments from four small lake basins was determined and used as evidence for vegetation change on the Allegheny Plateau of southwestern New York State. The sites studied are within 35 mi of the unglaciated Salamanca reentrant and are on an important migration route for species spreading northward following Late Wisconsin glaciations.

Forests of the hemlock-northern hardwoods type occur in southwestern New York at the present time. Point-quarter sampling of upland stands shows *Acer saccharum, Fagus grandifolia,* and *Tsuga canadensis* to be the leading species in order of decreasing importance values. An analysis of bearing-trees recorded in the original lot survey notes for the areas around three of the sites studied palynologically revealed the precolonial forests to be dominated by the same leading species, except *Fagus* was first in importance and *Acer* second. R values were calculated using the precolonial data and a recent survey of existing timber resources in the region.

The basins studied include the Genesee Valley Peat Works in central Allegany County — on Olean drift (pre-Cary), Allenberg Bog in east-central Cattaraugus County — near the Kent terminal moraine (pre-Cary), and Houghton and Protection bogs in southeastern Erie County — on Valley Heads drift (= Port Huron?). The profiles obtained were divided into A, B, and C zones following the Deevey classification. In addition, a T zone characterized by high nonarboreal pollen (NAP) percentages occurs at Allenberg Bog. The T zone pollen assemblages compare well with the modern pollen rain at Fort Churchill, Manitoba.

The A zones differ according to the age of the drift on which the basins are situated. Most unique was the Genesee Valley site where spruce (ca. 25 percent) occurs with abundant NAP (40 to 45 percent). Spruce values decrease upward. The significance of the assemblages is obscure, but taken at face value, the presence of an open vegetation type, perhaps similar to park-tundra, is indicated. At Allenberg Bog, fluctuations in *Fraxinus nigra* and *Quercus* percentages suggest correlation with climatic modifications associated with glacier advance and retreat. However, absolute pollen frequency data from this site indicate that the fluctuations occurred as a response to increasing deposition rates for pine and spruce pollen. Wood near the bottom of zone A at Houghton Bog has been dated at 11,880 ± 730 B.P. (I-3290). Upper A zone spectra, except for the presence of pollen from temperate deciduous trees, are similar to surface spectra occurring today in the boreal woodland of central Quebec.

The spruce woodland disappeared around the Valley Heads sites about 10,500 years ago and was replaced by B zone forests dominated by *Pinus Strobus*. At several sites, lower pine-birch and upper pine-oak subzones can be distinguished. At Protection Bog, where the pine peak has been dated at 9030 ± 150 B.P. (I-3551), a *P. Strobus* cone was recovered from sediments deposited about 10,500 years ago.

Zone C-1 records the development of hemlock-northern hardwoods forests. With the exception of gradually increasing *Fagus* values, the profiles demonstrate stability in the regional vegetation during the interval between about 8000 and 4400 B.P. An abrupt decline in hemlock percentages marks the end of pollen zone C-1, which is dated at 4390 ± 110 B.P. (I-3550) at Protection Bog.

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[1] Submitted for publication May 19, 1969. Accepted for publication May 5, 1972.

[2] This study, in somewhat different form, comprised most of a thesis submitted to Michigan State University in partial fulfillment of the requirement for the Ph.D. degree. An abstract has previously appeared (Miller, 1969).

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Increased relative numbers of *Acer saccharum, Betula, Carya, Fagus,* and *Quercus* pollen types occur in zone C-2. *Tsuga* percentages remain low. Absolute pollen frequency determinations affirm the C-1/C-2 hemlock decline but show only slight increases in the numbers of broadleaf tree pollen types being deposited. This fact and the tendency for hemlock to exhibit high drought mortality may indicate a series of severe droughts occurring over a relatively short time span.

Zone C-3 which began 1270 ± 95 years ago (I-3549) at Protection Bog was divided into the following subzones: C-3a across which *Tsuga* pollen regains its position of prominence in the profiles and C-3b in which abruptly increasing percentages of NAP, including *Ambrosia, Plantago,* and *Rumex,* record European settlement and attendant forest clearance.

ACKNOWLEDGMENTS

The assistance of the following is gratefully acknowledged: Aureal T. Cross, Professor of Geology, Michigan State University, for advice and assistance with various phases of the study; John H. Beaman, Curator of the Beal-Darlington Herbarium at MSU for use of the facilities; my father, George C. Miller, for aid in collecting sediment samples; Robert Stickney and Arthur Flick, foresters with the New York State Department of Environmental Conservation for help in locating suitable forest stands; J. Gordon Ogden, III, Dalhousie University; Ernest H. Muller, Syracuse University; and Donald M. Lewis, New York State Museum and Science Service, for critical reading of the manuscript. My wife, Heather, has provided much encouragement and aided in preparation of the typescript. Financial support came from an NDEA Title IV Fellowship and by a Michigan State University Graduate Council Fellowship. Field expenses and funds for radiocarbon dating were provided by a New York State Museum and Science Service Graduate Student Honorarium.

Introduction

This report treats a problem that is historical in nature — vegetation change through time following deglaciation. The region involved is in western New York State where surfaces, according to available data, have been ice-free for at least 12,500 years, or longer southward toward the Pennsylvania border. Temperate broadleaf-deciduous or deciduous-coniferous forests now characterize the region. The history of their development as well as information on vegetation types that no longer exist in the area are major objectives in this investigation.

The principal technique used is pollen analysis whereby the vertical succession of pollen and spores is determined in sediments that have been accumulating in small lake basins for thousands of years. Changes in relative and absolute frequency of various pollen types through time serve as the basis for inferences concerning the history of past vegetation. When possible, supplemental data from other kinds of plant fossils are also included. Present forests of western New York must serve as reference points to which comparisons of past vegetation can be directed. Therefore, the existing forest vegetation of the region will be treated in some detail. In addition, certain historical records are used to develop a record, however incomplete, of the character of forests prior to the arrival of European man. Pollen analysis also provides a way to determine former climates because major vegetation classes presumably develop in response to regional climates.

The unglaciated Allegheny Plateau and Appalachian Mountains doubtless served as a refuge for many species of plants during Pleistocene glaciations, so southern New York State is a particularly critical area in which to conduct research of this kind. It is along an important migration route for species that participated in the revegetation of glaciated eastern North America.

The Region

For purposes of this report, southwestern New York State includes Cattaraugus, Chautauqua, Allegany, and southern portions of Erie and Wyoming Counties. However, because the whole of western New York forms a coherent unit historically, vegetationally, and otherwise, this area, which includes Genesee, Niagara, and Orleans Counties in addition to those already named, will be emphasized in the introductory material that follows.

The eight-county region (see figure 1) includes nearly 6550 square miles. It lies between 42° 00′ and 43° 25′ N. lat. and 77° 45′ and 79° 45′ W. long., or in more general terms, extends southward from Lake Ontario nearly 100 mi to the Pennsylvania border and eastward from Lake Erie and the Niagara River 65 to 100 mi depending on the latitude, to the Genesee River. The counties along the Pennsylvania border are by far the largest in area, though least in population. At present the greatest concentration of population occurs at Buffalo and extends northward into the southwestern corner of Niagara County.

As political units, the counties date from the early part of the 19th century. Prior to this time, the region was visited by few Europeans, although in 1679, slightly more than 50 years after the formation of the Plymouth Colony in Massachusetts, an expedition under Robert Cavelier de La Salle established a short-lived outpost at the mouth of the Niagara River (Williams, 1947). It wasn't until 1720, however, that the region had its first permanent resident and not until the late 18th century and early 19th century that more than a handful of settlers were present. In 1810, for example, there were only about 16,000 inhabitants in the eight-county region, but a decade later the population totaled about 75,000 and hardly any district lacked the beginnings of settlement (Meinig, 1966).

Before arrival of settlers of European descent, western New York was occupied by a succession of Indian tribes. The Iroquois controlled much of the state prior to the Revolutionary War, and the Senecas, one of five original Iroquois tribes, originally occupied the region between Cayuga Lake and the Genesee River, but later extended their influence to Lake Erie and the Niagara River by conquering the Erie and Neutral tribes which previously controlled these areas. The Iroquois generally lived in stockaded villages containing about 250 people. Their homes were often surrounded by small, partially cleared fields where corn, beans, and squash were cultivated. It has been estimated that about 20,000 Iroquois lived throughout New York State during the 18th century (Rayback, 1966). While a complete summary of the archeology of Iroquoian and pre-Iroquoian Indians in New York has been provided by Ritchie (1969), the effect of aboriginal hunting and agricultural practices on the vegetation of western New York is little known.

Today, outside the growing urban centers of the region, farming constitutes the largest percentage of land use. The most heavily cultivated areas occur in Niagara, Orleans, Genesee, and northeastern Erie Counties and in a narrow strip in Chautauqua and southern Erie Counties immediately adjacent to Lake Erie (Thompson, 1966). Vegetables and fruits are the principal crops throughout this region. Niagara and Orleans Counties contain the highest percentages of nonforest land — 83 percent and 80 percent, respectively (see table 2, p. 14). Southward, but north of the Allegheny River and southeastern Allegany County, dairy farming and the supportive growing of feed crops for cattle accounts for most of the land use. Here, and in the largely nonagricultural lands of southern Cattaraugus and Allegany Counties, secondary forest covers about 60 percent of the area.

PHYSIOGRAPHY

Extending southward from Lake Ontario to southern Genesee and east-central Erie Counties, thence southwestward along the south shore of Lake Erie, in a strip about 15 mi wide in central Erie County and about 2 mi wide at the Pennsylvania border (figure 1), is the Erie-Ontario Lowland, one of two principal physiographic regions of western New York State. The lowland is mostly underlain by easily-eroded shales, although two prominent east-west trending limestone escarpments occur in the area adjacent to Lake Ontario. These features subdivide this part of the low-

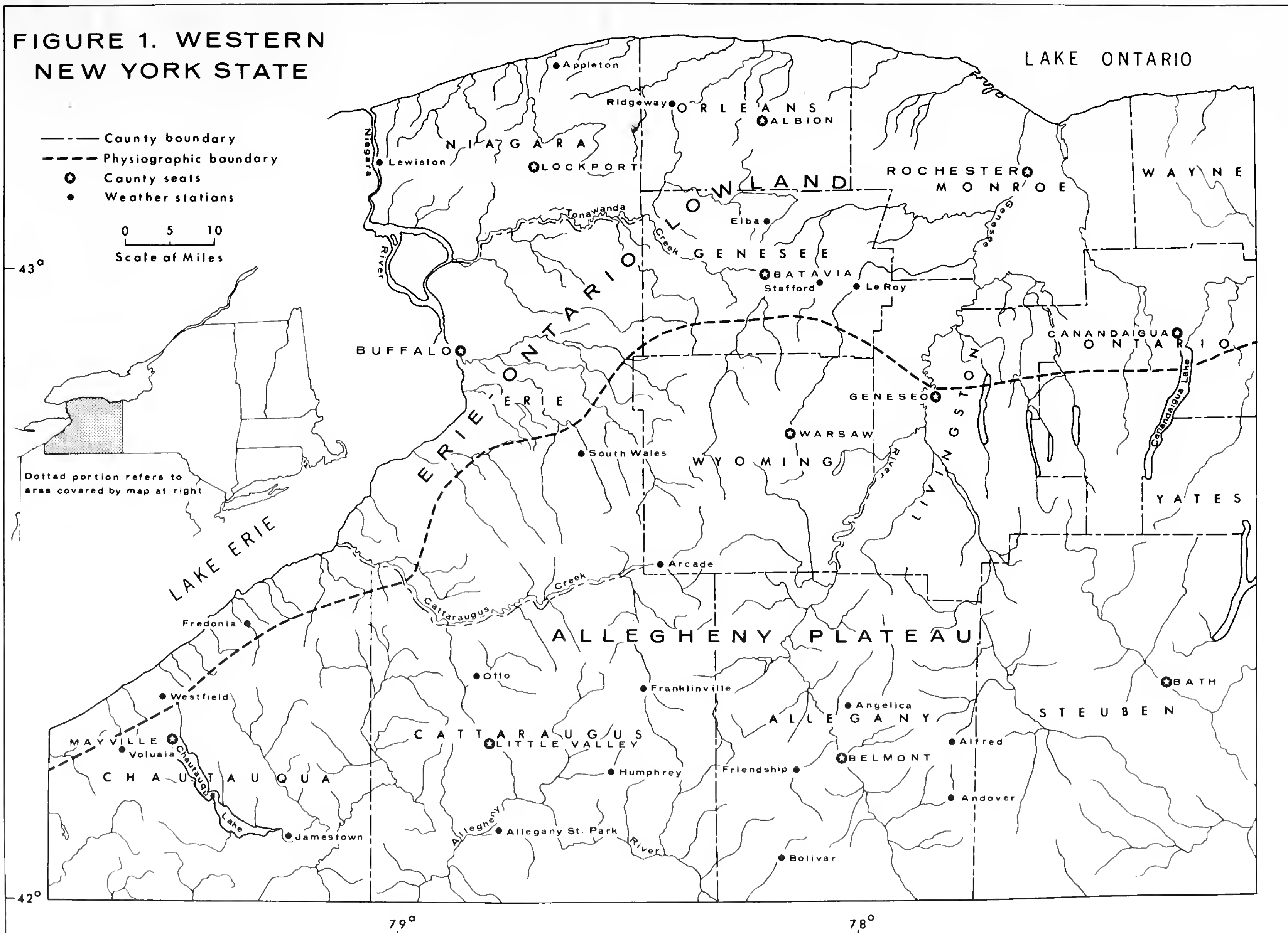


FIGURE 1. WESTERN NEW YORK STATE

land into three more or less flat plains which are in part covered by lacustrine sediments deposited during ancestral stages of Lakes Erie and Ontario.

The Allegheny Plateau or Appalachian Upland, the other main physiographic region of western New York, is bounded on the north by the Portage escarpment. Elevation and relief increase southward, and the highest point in western New York, 2,548 ft, is found near Bolivar in southern Allegany County. The plateau is usually divided into glaciated and unglaciated sections. Southeastern Chautauqua, southern Cattaraugus, and southwestern Allegany Counties, an area approximately bounded by the Allegheny River, were apparently never completely invaded by ice. Muller (1963) points out that the unglaciated region is characterized by less smoothly eroded ridges, more continuous crest lines, and deeply incised V-shaped valleys. He further notes that as far as 15 mi north of the limit of glaciation, summit reduction by glacial scour was as little as 50 to 100 ft although, farther to the north, greater lowering occurred. Throughout most of southern New York less than 200 ft of bedrock was removed from the plateau tops (Muller, 1964a).

The drainage of western New York is generally northward into the St. Lawrence River (figure 1). Streams in only the southern portions of Chautauqua and Cattaraugus Counties and the southwestern corner of Allegany County empty into the Allegheny River which is connected to the Mississippi by way of the Ohio River. The drainage divide separating the St. Lawrence and Mississippi watersheds extends northeastward in Chautauqua County approximately following the crest of the Lake Escarpment moraine, several miles inland from Lake Erie. From there, it may be followed eastward across northern Cattaraugus County with a dip southward toward Little Valley and, finally, southeasterly across eastern Cattaraugus and western Allegany Counties. Part of eastern Allegany County is drained eastward into Susquehanna River.

The only large inland lake in the region is Lake Chautauqua, which occupies the axis of a through valley in south-central Chautauqua County. A number of smaller lakes exist and many of these developed in kettles by melting of partly buried ice blocks. Several artificial lakes occur in lowland areas and along the beds of major rivers and streams.

BEDROCK GEOLOGY

Western New York State is entirely underlain by Paleozoic sedimentary rocks (Fisher *et al.,* 1961) which are exposed at the surface in only limited areas. The beds dip gently to the south so that rocks of greater age are encountered successively northward. More or less east-west trending belts of shale, siltstone, and sandstone are present throughout the region, but the most important exposures of limestone and dolomite are found in the lowland north of the Allegheny Plateau. Complete summaries of the bedrock geology of Erie and Chautauqua Counties have been published by Buehler and Tesmer (1963) and Tesmer (1963), respectively.

Red shales and siltstones of Late Ordovician age outcrop in the area adjacent to Lake Ontario and are the oldest rocks exposed in the region. To the south, the predominantly calcareous deposits comprising the Niagara escarpment accumulated during Middle Silurian time, while farther southward still, the Onondaga escarpment is composed of limestone deposited during the early part of Middle Devonian time. The 10 miles separating the two zones of calcareous rock are mostly occupied by weak shales, Late Silurian in age. Later in Middle Devonian time, shales replace limestones. Upper Devonian rocks, mostly siltstones and shales, subordinate sandstones, and rarely conglomerates and thin limestones are found southward from central Erie and southern Genesee Counties. Near the Pennsylvania border, largely within the unglaciated portion of western New York, occur Lower Mississippian and Lower Pennsylvanian shales, sandstones, and conglomerates. These deposits have been greatly dissected by erosion and may be considered outliers of more continuous strata of the same age to the south. Muller (1963) suggests that the resistant conglomerates in this area may have terminated southward glacial movement.

GLACIAL GEOLOGY

In contrast to the age relationships of the bedrock units, surficial deposits resulting from Pleistocene glaciations are oldest in the south and youngest in the north. Only drift from Illinoian and Wisconsin glaciations has been identified in western New York, although study of the development of the present Allegheny River indicates pre-Illinoian glacial activity (Muller, 1963, 1965).

The earliest recognized deposit of Wisconsin age is the Olean drift which in western New York is found at the surface on the north and east sides of the unglaciated portion of the Allegheny Plateau (figure 2). This roughly triangular area, often referred to as the

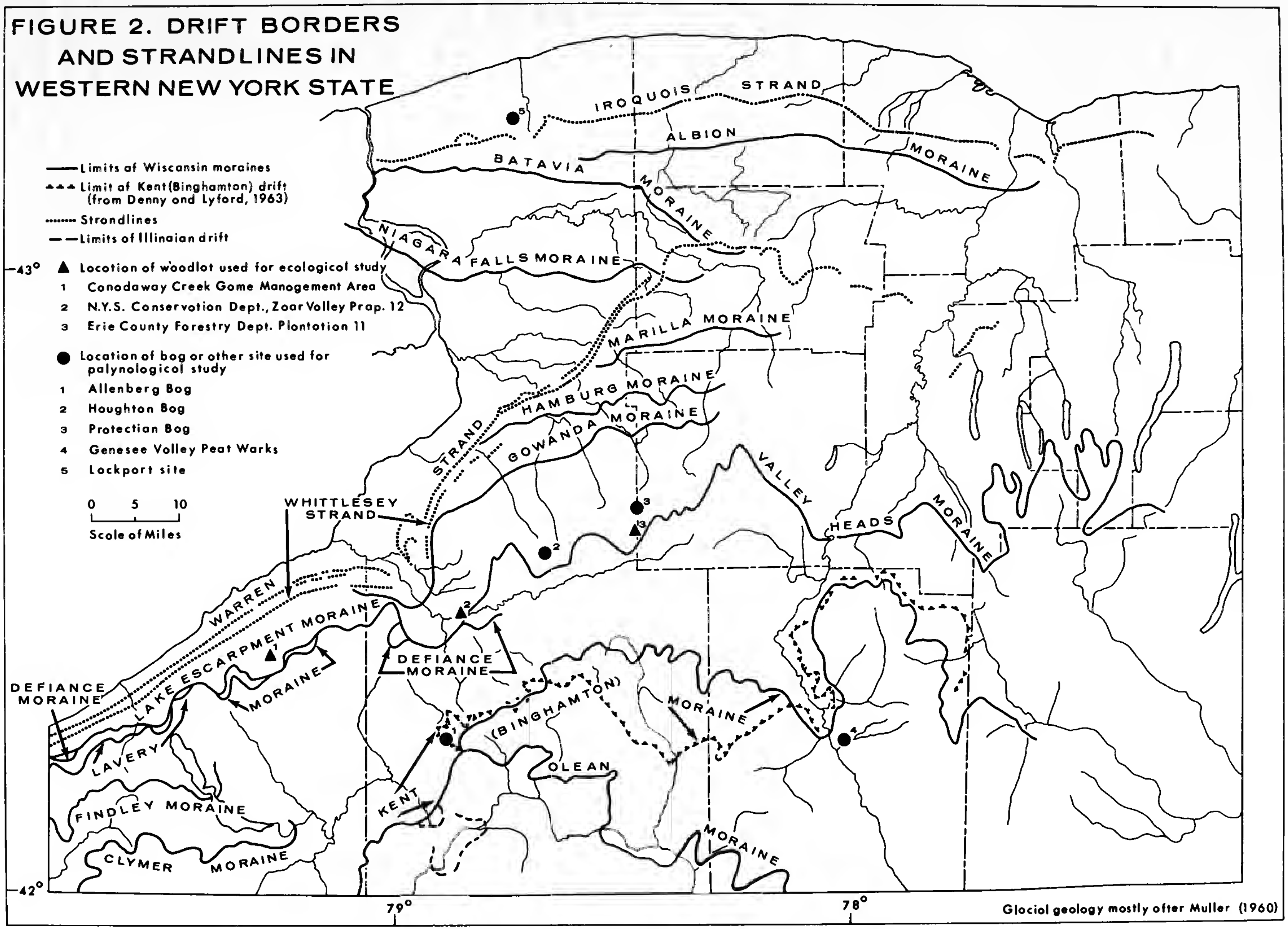


FIGURE 2. DRIFT BORDERS AND STRANDLINES IN WESTERN NEW YORK STATE

Salamanca reentrant, is located at the junction of deposits produced by ice moving southeastward out of the Lake Erie basin and similarly derived deposits from the north and east from the Lake Ontario basin. Olean drift as mapped by MacClintock and Apfel (1944; however, cf. Denny & Lyford, 1963) forms the terminal moraine on the north and east sides of the reentrant and follows a greatly convoluted course extending slightly south of east from about 3 mi northeast of Napoli to near Humphrey where its position extends abruptly southward toward the village of Allegany. From this point, it angles southeastward toward the corner of Cattaraugus County. It is a very subdued terminal moraine but the limit of glaciation can be determined by the presence of erratic cobbles (Muller, 1965). The exact age of the Olean moraine is not known. MacClintock and Apfel (1944) consider it Iowan or Tazewell in age; other authors concur with this disposition. However, Denny and Lyford (1963) point out that it may be a pre-Farmdale-post-Sangamon substage. There is, at any rate, general agreement that it is pre-Woodfordian in age.

A section exposed near the village of Otto in northwestern Cattaraugus County displays evidence of a long history of successive glaciations now considered to have occurred entirely within the Wisconsin Stage (Muller, 1964b). Near the base of the section and in association with Olean drift (Denny & Lyford, 1963) are peats, initially determined to be more than 35,000 years old (W-87; Suess, 1954) but later to have a finite age of 63,900 ± 1700 B.P.[4] (GRN-3213; see Muller, 1964b), which have been correlated (Muller, 1965) with deposits of the early Wisconsin St. Pierre Interstade in the St. Lawrence lowland (see Terasmae, 1958). The several distinct peaty layers which make up the Otto organic deposit have been examined for pollen by four workers whose results are available in Muller (1964b). The pollen assemblages obtained indicate that the vegetation surrounding the site was similar to that found today in the boreal forest of Canada, roughly 50 mi north of North Bay, Ontario. Upward in the section, rhythmites alternate with layers of till. The former represent separate developments of glacial Lake Zoar, and the latter, repeated invasions of ice sheets correlative with the "classical" Wisconsin glacial advances.

On the west side of the Salamanca reentrant, the terminal moraine is formed of Kent drift. The basic distinctions between it and the Olean drift to the east have been described by MacClintock and Apfel (1944) who note that the former is characterized by unmodified constructional topography and a relatively high content of carbonates which are only shallowly leached. The Olean drift is less calcareous, the carbonates are more deeply leached, and there is a greater modification of its constructional topography. The Kent terminal moraine, as mapped by MacClintock and Apfel (1944; cf. Denny & Lyford, 1963), separates from the Salamanca reentrant at a point 3 mi northeast of Napoli where the westernmost deposits of Olean drift are encountered (figure 2). From there, it may be traced over a generally eastward course to near Belmont in central Allegany County from where the margin extends northward to a point near the Wyoming County line. It can be further traced southeastward across northeastern Allegany County but is lost in eastern Steuben County near Almond.

The name "Binghamton" was originally given to Kent drift because of its apparent equivalence to kame deposits near the city of Binghamton in south-central New York State, although this relationship has been questioned by Denny and Lyford (1963) and others. The Binghamton drift border in far southwestern New York State has been correlated with the Kent moraine of northwestern Pennsylvania and northeastern Ohio by continuous tracing (Muller, 1963). White *et al.* (1969) have recently stressed that the Kent moraine in northwestern Pennsylvania is cored with Early Wisconsin drift and that the Kent till is only a thin layer on top of this, extending at places beyond the mapped boundary of the moraine. This relationship may apply also to parts of western New York. A possible equivalent of the Kent moraine in the western Finger Lakes region, the Almond moraine, has been traced eastward from the Genesee River toward Bath by Connally (1964).

The minimum age of the Kent drift is provided by a radiocarbon date of 14,000 ± 350 B.P. for marl collected at the bottom of a kettle hole in Kent drift near Corry, Pennsylvania, 9 mi inside the Wisconsin drift border (W-365; Droste *et al.,* 1959). Although this age determination indicates the Kent glaciation may be early Cary in age, more recent study has shown it to be considerably older. From sections exposed near Cleveland, Ohio, White (1968) has obtained radiocarbon dates for two wood samples embedded in lacustrine sediments interpreted as having been deposited from a proglacial lake ponded in front of the advancing Kent ice. These age determinations, 24,000 ± 800 B.P. and 23,313 ± 391 B.P., imply that the Kent ice overrode this area about 23,250 years ago.

[4] Radiocarbon Years Before Present. In this report ages based on radiocarbon dating whether noted or not are in radiocarbon years which generally differ somewhat from calendar years.

A number of other moraines occur on the west side of the reentrant (Muller, 1963). These have been interpreted as recessional features developed during retreat of the ice sheet that produced the Kent (Binghamton) terminal moraine (Findley and Clymer moraines), or to mark a readvance of the ice margin following the northwestward retreat of the Kent ice (the Lavery moraine).

The well-marked Valley Heads moraine occurs to the north across midcentral and midwestern New York State. It is represented by a group of parallel morainic deposits at the edge of the Allegheny Plateau in western Chautauqua and southern Erie Counties where the complex is called the Lake Escarpment moraine. According to Muller (1965), mapping has established the equivalence of the Lake Escarpment and Valley Heads moraines. Woody detritus, 14,900 ± 450 years old (I-4216; Calkin, 1970), from a depression in the Chaffee outwash plain, which is located near the southeast corner of Erie County, provides a minimum date for withdrawal of ice from the distal edge of the moraine. Although the Valley Heads-Lake Escarpment moraine is often cited as equivalent to the Port Huron moraine in the Midwest, this relationship is now in question because radiocarbon dates on material associated with the Port Huron maximum are considerably less than 14,900 years old.

A series of moraines, most of which were first traced by Leverett (1902), occur north of the Valley Heads-Lake Escarpment complex. Many of these are not prominent topographically because deposition occurred in proglacial lakes where erosion was rapid. Northward they are the Gowanda, Hamburg, Marilla, Alden, Buffalo, Niagara Falls, Barre, Batavia, and Albion moraines. Most are illustrated in figure 2. A recently obtained radiocarbon date, 12,730 ± 220 B.P. (I-3665; Calkin & McAndrews, 1969), which provides a minimum date for recession from the Gowanda moraine, has lead Calkin (1970) to suggest that deposition of either the Gowanda or Hamburg moraine may correlate with the Port Huron maximum. Studies of sediments in Lake Erie support the contention that the Port Huron equivalent in western New York represents a major readvance of glacier ice. A fluvially eroded drift sheet identified beneath the waters of modern Lake Erie by seismic reflection and believed to be of Cary (Lake Border) age indicates that drainage was eastward probably over the Niagara escarpment during the Cary-Port Huron Interstade (Wall, 1968). This could only have taken place if the glacier margin was north of this point.

Final withdrawal of glacier ice from western New York must have been rapid, for a series of radiocarbon dates associated with sediments of Lake Iroquois, which developed in the Lake Ontario basin north of the Albion moraine, average 12,000 B.P. (Goldthwait *et al.*, 1965; Karrow *et al.*, 1961). By this time the ice margin had melted to an unknown distance north of the Niagara escarpment and may have freed much of the Lake Ontario basin, although the St. Lawrence lowland was still blocked. New York State was apparently not invaded by Valders ice (MacClintock & Terasmae, 1960; Terasmae, 1959).

Beaches and strand lines marking the shorelines of the ancestral stages of Lakes Erie and Ontario are found in northwestern Chautauqua County and from central Erie and Genesee Counties northward. This subject is treated in detail by Hough (1958, 1963). Calkin (1970) has recently summarized the chronology of the glacial Great Lakes in reference to his own work in northwestern New York State.

SOILS

The soils of western New York, with the possible exception of those found in the Salamanca reentrant, are relatively young because they have been formed from surface material in a region that was ice-covered during the Wisconsin glaciation. These soils are distributionally related to and mostly derived from the east-west trending bedrock units of the area. However, due to the direction of ice movement and the intensity of glacial scour, there has been a general distribution of parent material southward. As a result, the limestone and dolomites of the Erie-Ontario Lowland are found not only in the drift that mantles the lowland plains but also along the northern edge of the Allegheny Plateau. The amount of calcareous material transported away from the lowland gradually decreases toward the Pennsylvania border permitting a distinction to be made between the predominantly limy soils of northern western New York and the acid ones of the southern upland.

New York State is in a transition zone between cool, humid climates which generally produce podzols and climates characterized by warmer temperatures which favor the formation of gray-brown podzolic soils (Cline, 1955). Although soils of the latter type predominate at the west end of the state, podzols occur in southwestern Allegany, southern Cattaraugus, and southwestern Chautauqua Counties. The region directly

south of Lake Ontario encompassing Niagara, Orleans, and the northern part of Genesee Counties is broadly categorized as an area of intrazonal soils. Gray-brown podzolic soils are located in the intervening region (Soil Survey Division, 1938). Further details, including descriptions of the soil associations recognized in New York State, are found in Cline (1955).

Little work has been done in western New York relating soils and vegetation. It has been pointed out that there is an approximate equivalence between the Hemlock-white pine-northern hardwood forest region and the area characterized by podzols, and that a similar relationship holds for the Eastern deciduous forest and the region of gray-brown podzolic soils (Braun, 1950; Gordon, 1940). However, the boundary separating the two major vegetation units in western New York (Braun, 1950) is the Portage escarpment — deciduous forests occupy the lowland adjacent to Lakes Erie and Ontario while coniferous-deciduous forests are situated on the upland. The podzol/gray-brown podzolic boundary, in contrast, occurs far south of the escarpment.

The forest communities occurring on certain soils in Cattaraugus County have been described in less general terms by Gordon (1940) to which the reader is referred for information other than that presented here. On the higher parts of the plateau grow forests of hemlock, white pine, red maple, chestnut (now absent), sweet birch, and cucumber tree, while certain other podzols support forests dominated by hemlock and beech. Mixed mesophytic forests of red oak, beech, chestnut (now absent), red maple, sweet birch, white ash, black cherry, and often other species characterize thinner, drier podzols. Oak associations, originally containing chestnut, are found on the driest upland soils. Similar data from elsewhere in western New York have not been published.

CLIMATE

Warm to hot summers, cold winters, and adequate precipitation, typical of humid continental climates in general, characterize New York State. In the eight-county region, the terrain and nearby Lakes Erie and Ontario have a marked influence on the overall climate. During fall the lakes liberate heat, thereby lengthening the frost-free period, while at the end of winter they keep the surrounding area cool and delay plant growth until the danger of frost is past. Nearly all lowland areas have from 140 to 180 frost-free days. At higher elevations, however, the tempering effect of the lakes is less apparent, and southward, the length of the growing season decreases until 100 days or less is reached in southeastern Cattaraugus and southwestern Allegany Counties.

Specific differences in climate between upland and lowland sections of western New York are documented by data in table 1. Mean annual temperatures at stations in the Erie-Ontario Lowland are nearly uniformly 2–3° F higher than those in the upland. Plateau stations have recorded the lowest winter temperatures but both regions experience nearly the same summer maxima, although summers are generally cooler in the upland. High elevation and the comparatively dry atmosphere over the plateau combine to give high day and low night temperatures which result in an almost typical continental type of climate in this region (Mordoff, 1949).

The basic difference between energy reception in the upland and in the lowland is well illustrated by figures for potential evapotranspiration and growing degree months, which are higher in the lowland than in the upland (Carter, 1966). Plant distribution in western New York correlates well with these indices. Southern species are found principally in the lowland where the more favorable climate presumably ensures their survival, although other factors perhaps also exert some control.

Moisture is brought to New York State from the Gulf of Mexico and the Atlantic Ocean through the activity of cyclonic storms and, locally, Lakes Erie and Ontario are important sources of moisture also. Annual precipitation in the upland generally exceeds that in the lowland, often by 10 in or more. In western New York, per annum precipitation increases irregularly southward until a maximum of 48 in is reached in northwestern Cattaraugus County (Johnson, 1960) where, significantly, one of the largest areas of upland sphagnum bog occurs. The northern half of Niagara County and nearly all of Wyoming County, in contrast, are among the driest parts of the state.

Precipitation is fairly evenly distributed throughout the year, but summer months characteristically receive more than others. During the growing season, somewhat less rain falls in lowland areas than on the upland. Although summer is the season of greatest rainfall, it is also the time of greatest moisture need, so small moisture deficits occasionally occur. Few major droughts, however, have affected the region. A serious one occurred in 1899 when total precipitation for the three summer months was less than 3 in at localities

TABLE 1
Selected Climatic Data from Weather Stations in Western New York State by Physiographic Region *

Location	Mean Annual Temp.	Mean January Temp.	Mean July Temp.	Mean Growing Season † Temp.	Highest Temp.	Lowest Temp.	Ave. Date of Last Spring Frost	Ave. Date of First Fall Frost	Mean Annual Precip.	Mean Growing Season † Precip.
Erie-Ontario Lowland										
Appleton (300′) ‡	47.1	25.7	70.1	63.8	106	—13	May 4	Oct. 16	27.33	12.01
Buffalo (693′)	47.0	25.2	70.0	64.0	97	—20	Apr. 26	Oct. 22	35.16	14.57
Elba (750′)	45.7	23.4	69.7	63.4	100	—21	May 8	Oct. 6	36.72	15.21
Fredonia (750′)	48.6	27.6	71.3	65.4	98	—26	May 1	Oct. 21	36.72	16.89
Le Roy (900′)	46.1	23.2	68.9	64.0	99	—14	May 8	Oct. 6	36.45	15.86
Lockport (520′)	47.1	24.9	70.3	64.3	103	—24	May 5	Sept. 19	30.91	14.39
Ridgeway (420′)	47.4	24.8	71.3	64.9	96	—9	May 4	Oct. 3	32.98	16.79
Stafford (925′)	47.6	25.4	71.7	65.8	103	—33	May 12	Oct. 4	31.63	14.39
Intermediate										
South Wales (1073′)	46.0	24.5	69.5	63.7	103	—31	May 13	Oct. 1	38.99	16.25
Westfield (1050′)	47.7	25.1	70.2	64.6	98	—19	May 2	Oct. 21	38.53	18.91
Allegheny Plateau										
Alfred (1760′)	44.8	22.9	67.2	61.8	101	—35	May 18	Sept. 28	35.83	17.84
Allegany State Park (1500′)	45.6	25.2	66.6	61.7	101	—35	May 28	Sept. 18	42.82	19.95
Andover (1670′)	45.4	24.1	67.4	62.3	100	—34	May 21	Sept. 25	33.64	17.25
Angelica (1420′)	45.3	23.7	67.8	62.3	104	—40	May 25	Sept. 24	35.26	17.61
Arcade (1707′)	44.0	20.6	67.4	61.6	95	—38	May 22	Sept. 28	41.96	21.08
Bolivar (1800′)	45.1	22.9	66.7	61.5	101	—37	June 1	Sept. 17	39.83	19.87
Franklinville (1590′)	45.0	23.0	67.3	61.9	99	—45	May 21	Sept. 22	38.76	18.09
Humphrey (1951′)	45.4	22.7	68.3	62.8	93	—17	May 14	Sept. 25	44.45	22.30
Jamestown (1390′)	47.6	25.3	70.0	64.7	100	—31	May 12	Oct. 5	43.83	19.26
Otto (1260′)	46.8	23.3	69.7	64.3	99	—24	May 13	Oct. 16	33.09	16.79
Volusia (1560′)	45.6	23.4	68.4	62.9	98	—18	May 10	Sept. 22	38.53	17.26

* Data from Mordoff (1949); temperatures in degrees Fahrenheit, precipitation in inches.
† May 1 to September 30.
‡ Elevation in feet above sea level.

bordering Lake Ontario (Mordoff, 1949). There has been at least one noteworthy period of drought every 20 years.

FLORA

Floristic research in western New York State began in earnest during the mid-1800's. Before this time, however, Niagara Falls had attracted naturalists and plant collectors to the region, many of whom published botanical observations made at the Falls (see Dow, 1921) or while travelling across the Erie-Ontario Lowland. Unfortunately, most of this information seems to have been gathered casually or, in some cases, by untrained people, making its value questionable for purposes of defining the plant cover of the region. Three of the more notable visitors were Peter Kalm, who viewed the cataract in 1750 (Kalm, 1751), François André Michaux, who travelled throughout the eastern Great Lakes area in 1806 or 1807, and Thomas Nuttall, who undertook a pedestrian trip from Philadelphia to Canandaigua and west to Niagara Falls in 1809 (Graustein, 1967). Zenkert (1934), in addition to reporting a total of 1,587 species of vascular plants (1,187 native, 400 introduced) from within a 50-mile radius of Buffalo, has also traced the history of botanical exploration in western New York from early times through the 1930's.

Floristically, three more or less distinct regions are present in western New York. The Wisconsin terminal moraine (see figure 2), which approximately separates glaciated and nonglaciated districts, marks the southern limit of a group of boreal species, thereby defining the first region, the unglaciated upland. The species involved are mostly bog plants which presumably are not found south of the drift limit because kettle holes and other suitable habitats generally associated with glaciated terrain are absent.

The second and third floristic regions are delimited by physiography and correspond to the Erie-Ontario Lowland and the Allegheny Plateau. Typical upland species can occur on both sides of the glacial limit. The boundary between the two regions is usually depicted as part of the well-known tension zone that crosses Minnesota, Wisconsin, Michigan, southern Ontario, and extends across western and central New York to the eastern end of Lake Ontario. In New York State, it is mostly coincident with the Portage escarpment. The tension zone has not been studied extensively in central and western New York, and plant distribution maps similar to those which support its existence elsewhere are not available. However, in western New York, it is clear that the upland is characterized by species which are absent or are of greatly restricted occurrence in the lowland. Conversely, *Asimina triloba,*[5] *Celtis occidentalis, Nyssa sylvatica,* and others grow in the lowland or rarely on the flank of the Allegheny Plateau and are absent from higher portions of the upland. Zenkert (1934), who recognizes the distinction between the lowland and upland flora, lists 96 species which represent an austral element best developed in the region adjacent to Lakes Erie and Ontario. This distribution pattern is also the basis for Bray's recognition (1915) of two zones in western New York separated approximately by the Portage escarpment and characterized by different tree species. His Zone B, in which chestnut (now absent), oaks, hickories, and tulip-poplar are common, occurs across the lowland, while Zone C, characterized by sugar maple, yellow birch, hemlock, and white pine, corresponds in area to the Allegheny Plateau.

It is noteworthy that northern species are best represented on the plateau, while plants characteristic of southern regions are most common in the lowland, a situation directly opposite that found in Michigan and Wisconsin. In western New York, climate may be the major factor controlling this pattern, although soil and other edaphic factors probably have a role also. The more rigorous climate of the upland would tend to eliminate species adapted to higher mean winter temperatures and a longer growing season.

To further describe the nature and geographical relationships of western New York's flora, it can be divided into phytogeographic elements, each of which is made up of species that share a similar type of distribution pattern today. These species are typical of a certain natural area; that is, the entire geographical range of a taxonomic unit attained through natural dispersal mechanisms, whether it now grows within that area or not (Cain, 1944). Such species have the same center of dispersal, but may or may not share a common center of origin. The identification of elements in a regional flora is based upon their being characteristic of certain well-defined phytogeographical areas elsewhere. Elements may be categorized as either extraneous or intraneous. The former contains species at or near the limits of their ranges which may, therefore, exhibit disjunctions of various types, while the latter includes plants of widespread distribution whose occurrence in a particular region is well within the total range of the species (Braun, 1937; Cain, 1944). Intraneous species, which may comprise as much as 60 percent of a flora (Parker, 1936; Thompson, 1939), tell little about the affinities of that flora, but extraneous ones are considerably more helpful in this regard.

The Alleghenian element (see Curtis, 1959) contains a group of species of Arcto-Tertiary origin which center in the southern Appalachians and extend northward into southern Canada. Such well-known and important forest trees as *Acer saccharum, Betula alleghaniensis, Fraxinus americana, Pinus Strobus, Quercus alba, Tilia americana,* and *Tsuga canadensis* are members of this element. Also of Tertiary origin is the Ozarkian element which contains more drought tolerant species developed in isolation from the southern Appalachians on the Ozark upland of Missouri and Arkansas. *Acer saccharum* var. *nigrum, Carya* spp., *Quercus macrocarpa, Q. Muhlenbergii,* and *Q. velutina* are components of this element. For certain other species now found in western New York (e.g., *Magnolia acuminata*), both the Appalachians and the Ozarks presumably acted together as a single center of origin and dispersal (see Steyermark, 1939).

Members of the Boreal element are not rare in western New York, but, in most cases, they occupy restricted positions in bog communities developed in undrained depressions. *Abies balsamea, Larix laricina,* and *Picea mariana* are members of this element. These trees are characteristic of the boreal forest which ranges across central Canada from eastern Alaska to the Atlantic seaboard and south to the upper Great Lakes. Another group of species characteristic of northern regions but often found southward in the mountains belongs to the Arctic-alpine element. As expected, it is very poorly represented in western New York but has better expression in the Adirondack and Catskill Moun-

[5] Plant nomenclature throughout this report follows Fernald (1950) with the exception of binomials used for yellow birch and leatherleaf which are *Betula alleghaniensis* Britton and *Cassandra calyculata* (L.) D. Don, respectively.

tains to the east. *Pinguicula vulgaris* and *Saxifraga aizoides,* which grow together near a falls of the Genesee River in southeastern Wyoming County (their only station at the west end of the State; Zenkert, 1934), are members of this element.

Species typical of western North America but also found eastward are members of what can be broadly called a Western element. Actually, this category includes several distinct distribution patterns, two of which in particular pertain to western New York. The Prairie element is made up of species whose ranges center on the existing prairies. Certain members of this element such as *Andropogon Gerardi, A. scoparius,* and *Sorghastrum nutans* now have a wide distribution across the Erie-Ontario Lowland where they are generally found in abandoned fields, in hedgerows, and in thin, second growth oak stands often associated with prairie forbs. Prior to settlement, these species apparently grew in prairie-like oak openings characteristic of the lowland. Shanks (1966) felt that the oak openings in this area were essentially edaphic prairies, remnants of more extensive grasslands which occurred in this region at some time in the past. The shallow dry soils and the occasional water deficits characteristic of the Erie-Ontario Lowland favor persistence of prairie species and exclude more mesophytic competitors. A Cordilleran or Western Mountain element was early recognized in eastern North America by Fernald (1925), and more recently Iltis (1965, 1966) has redirected attention to it, pointing out that ". . . the ranges of many of our commonest as well as rarest species in the northeastern United States . . . fall into the standard pattern of eastern North America — western North America vicarious species pairs with the post-glacially produced modern ranges overlapping in glaciated northeastern North America " (1965, p. 149). As examples, Iltis (*ibid.*) cites a substantial list of paired species of which *Actaea rubra* (western) and *A. pachypoda* (eastern), among others, both occur in western New York.

Having a limited distribution along the beaches of Lakes Erie and Ontario and westward around the upper Great Lakes are species which belong to the Atlantic Coastal Plain element (Peattie, 1922). These species apparently attained their current ranges sometime during late or postglacial time, perhaps by migrating along the St. Lawrence or Mohawk River valleys and thence along the shores of the ancestral Great Lakes. *Cakile edentula, Euphorbia polygonifolia, Lathyrus maritimus,* and *Xyris caroliniana* are a few Coastal Plain species found in our area.

Also present in western New York is an exotic element, containing non-native species which have entered the region through the activities of man. Of particular interest to the pollen analyst are certain species of *Plantago* introduced from Europe, especially *P. lanceolata* and *P. major.* The appearance of *Plantago* pollen in postglacial sediments, which mostly can be attributed to these species, clearly marks the arrival and spread of Europeans in America. About 25 percent of the flora within 50 miles of Buffalo is comprised of introduced species.

VEGETATION

General Statement

Authors of the earliest histories published about western New York are uniform in stating that the region was completely wooded at the time of settlement except for discontinuous openings in the oak forests of the Erie-Ontario Lowland and other small partially cleared areas associated with Indian villages.

The observations of an accomplished botanist, Rev. E. J. Hill, while made four to six decades after clearing began, provide an accurate description of the forest cover of western New York. Rev. Hill was born at Le Roy in Genesee County in 1833 and spent much of the early part of his life in this region at a time when undisturbed tracts of forest were still fairly abundant. Hill (1895) reports that:

> The most abundant trees of the upland woods are the Beech and Hard Maple. On light soils, and where there is a considerable mixture of sand or gravel with the clay loam, the Oaks predominate, interspersed with Hickory, and sometimes with the Chestnut. In colder and higher tracts or along the banks of streams, the Hemlock is frequent or even abundant. The Basswood is common in the richer uplands, among Beeches and Maples. Here also the White Ash is most often seen. . . .
>
> Where the Beech and Maple abound the White Oak is occasionally mixed with them, but is mostly confined to the low land, where it is much more common than the Swamp White Oak. The Red Oak is much more commonly seen with the Beech and Maple. In flinty and gravelly soils the most common Oaks are the White, Red and Black Oaks. Here also occurs the Chestnut Oak; it is usually less abundant than the other kinds and may also be found in the wet lands (p. 382).

Turning briefly to historical records which pertain to either of the two physiographic regions, an account of the original timber covering of Orleans County indicates in a general way the nature of the forests through-

out the Erie-Ontario Lowland during the period of European settlement (Thomas, 1871).

> In its natural state Orleans County was thickly covered with trees. On the dry, hard land, the prevailing varieties of timber were beech, maple, white, red and black oak, white wood or tulip tree, basswood, elm, hickory, and hemlock. Swamps and low wet lands were covered with black ash, tamarack, white and yellow cedar, and soft maple; large sycamore or cotton ball trees were common on low lands and some pine grew along Oak Orchard Creek, and in the swamps in Barre; and a few chestnut trees grew along the Ridge [Lake Iroquois strandline] in Ridgeway, and in other places north of the Ridge (p. 29).

In comparison, C. G. Locke's description of the forests of Cattaraugus County, which pertains to much of the western Allegheny Plateau in New York State, emphasizes the prevalence of hemlock and pine in this region at the time of settlement (*in* Adams, 1893).

> This table-land was originally covered with a heavy growth of deciduous trees intermixed with hemlock and some pine, and this same description of the original forest would apply to the entire northern portion of the county, excepting that pine was generally found along the low-lands. The southern part of the county was covered with forest of the choicest pine and hemlock, with a mixture of deciduous trees. Here we find the home of the white and red oak and chestnut, which apparently did not cross the dividing ridge, as very little of this timber is found in the northern part of the county (p. 50).

These passages clearly indicate that, in general, forests of the lowland and upland were of a different type with beech, maple, oaks, and other deciduous species predominating in the former, while a mixed forest of conifer and deciduous trees occurred in the latter. Most botanists who studied the vegetation of this region in more recent years have also made this distinction. For example, Küchler (1964) recognizes three main types of forest in western New York (see figure 3, map A): (1) Beech-maple forest dominated by *Acer saccharum* and *Fagus grandifolia;* (2) Northern hardwoods forest dominated by *Acer saccharum, Betula alleghaniensis, Fagus grandifolia,* and *Tsuga canadensis;* and (3) Appalachian oak forest in which *Quercus alba* and *Q. rubra* are dominant, but generally occur with many other subdominant species. The boundary between (1) and (2) roughly corresponds to the Portage escarpment with the Northern hardwoods forest area in the upland and the Beech-maple forest area in the lowland, although inclusions of one type are mapped in the other and vice versa. The Appalachian oak forest is restricted to the Allegheny River Valley and to several small areas in the upland north of the Salamanca reentrant and adjacent to the Genesee River. It occurs more widely in the region of the Susquehanna River drainage immediately to the east of the area treated in this study.

Küchler has drawn heavily on the map of major forest types in Armstrong and Bjorkbom's study (1956) of the timber resources of New York State. Although the boundaries of the units being mapped are essentially the same in both publications, the units themselves differ somewhat. This is a result of two different approaches used in the preparation of the maps. In one case, the potential natural vegetation, or "the

TABLE 2

TOTAL AREA, NONFOREST LAND AREA, AND FOREST LAND AREA OF WESTERN NEW YORK STATE BY COUNTIES*

Counties	Total Land Area†	Nonforest Land Area		Forest Land Area			
				Noncommercial §		Commercial	
		Acres‡	Percent	Acres‡	Percent	Acres‡	Percent
Chautauqua	691.2	343.0	49.6	1.8	0.3	346.4	50.1
Cattaraugus	854.4	326.1	38.2	61.3	7.2	467.0	54.7
Allegany	670.7	259.4	38.7	2.5	0.4	408.8	60.9
Erie	674.7	468.4	69.4	2.5	0.4	203.7	30.2
Wyoming	382.7	259.8	67.9	6.6	1.7	116.3	30.4
Niagara	341.1	283.0	83.0	0.1	0.0	58.0	17.0
Genesee	320.6	227.1	70.8	1.3	0.4	92.2	28.8
Orleans	253.4	202.5	79.9	1.2	0.5	49.7	19.6

* Data from, "Preliminary forest survey statistics by counties and units, New York — 1967," Northeastern Forest Experiment Station, U.S. Forest Service, Upper Darby, Pennsylvania.

† In thousands of acres.

‡ Times 1000.

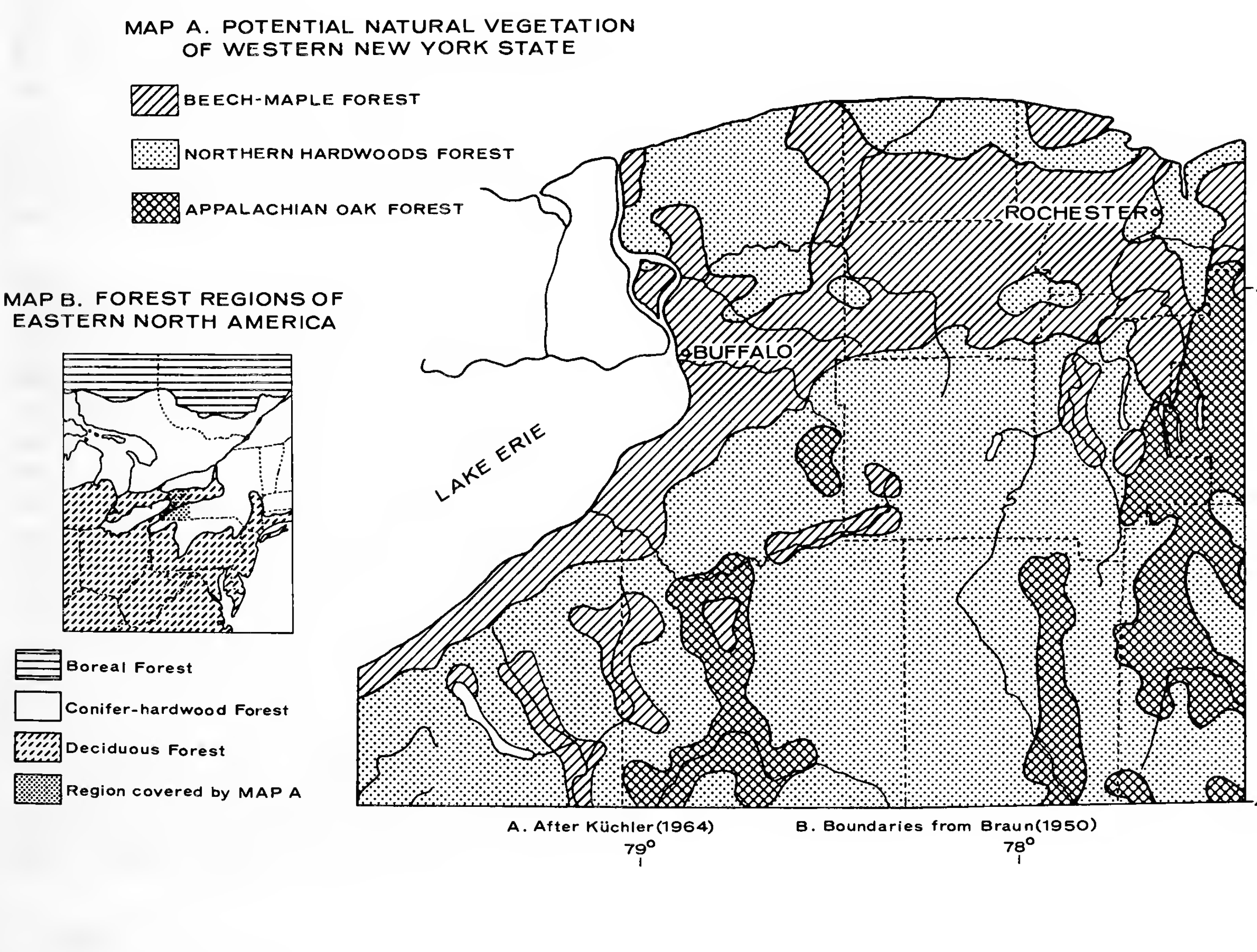
§ Includes nonproductive and productive but reserved forest land.

vegetation that would exist today if man were removed from the scene and if the resulting succession were telescoped into a single moment" (Küchler, 1964, p. 2), is mapped, while in the other, the actual or "real" vegetation determined by a survey of existing forests (during the period 1949–1952) is represented. Armstrong and Bjorkbom's work tells us what the general pattern and composition of existing forest vegetation is and, for this reason, a brief discussion of their units and those of Küchler follows. The area of currently existing forests in western New York is given in table 2.

The Northern hardwoods forest is distributionally equivalent to the Maple-beech-birch forest type of Armstrong and Bjorkbom. Maple-beech-birch forest is mapped as occurring widely across the upland but having a more restricted distribution in the lowland. It is made up of stands in which 50 percent or more of the trees are *Acer saccharum, Betula alleghaniensis,* and *Fagus grandifolia,* either singly or in combination. In addition, *Pinus Strobus, Tilia americana, Tsuga canadensis,* and *Ulmus* sp. often occur in such stands. Similarly, the Beech-maple forest region of Küchler is nearly the same as Armstrong and Bjorkbom's region of Elm-ash-maple forest, which is composed of stands in which 50 percent or more of the trees are *Acer rubrum, Fraxinus* sp., and *Ulmus* sp., by themselves or together. The widespread occurrence of this forest type north of the Portage escarpment today indicates the prevalence of swamp forests in the lowland. The Appalachian oak forest of Küchler is areally equivalent to the Oak-hickory forest of Armstrong and Bjorkbom. In the latter type of forest, 50 percent or more of a stand is in oak species.

Limited areas of other types of forest not noted by Küchler are also recognized by Armstrong and Bjorkbom. Small tracts of the White-red pine type are mapped southwest of Lake Chautauqua and along Cattaraugus Creek in southern Erie and northern Cattaraugus Counties. White pine is the dominant species in stands of this type and common associates include *Tsuga canadensis, Populus* spp., *Betula* spp., and *Acer* spp. Native red pines are very rare in western New

FIGURE 3. VEGETATION MAPS



A. After Küchler (1964)   B. Boundaries from Braun (1950)

York. Small areas typed as Aspen-birch forest occur in the Cattaraugus Creek Valley just west of the white-red pine area, in south-central Erie County, and in north-central Allegany County. These forests contain mainly aspen because, of the two birch codominants listed, only *Betula papyrifera* is native to western New York and is a rare species that does not occur in either area of Aspen-birch forest (see Zenkert, 1934). The other birch, *Betula populifolia,* is found eastward from central New York State to New England.

The distinction between the deciduous forest of the lowland and the coniferous-deciduous forest of the upland is discussed more fully by E. Lucy Braun (1950) in her monograph on the forests of eastern North America. As depicted by Miss Braun, the boundary separating these two forest types also coincides with the Portage escarpment (see figure 3, map B). The Beech-maple forest region (which is mapped as extending from central Indiana, southern Michigan and western Ohio; around Lake Erie, and across southern Ontario and northeastern Ohio to northwestern New York State) is located north of the escarpment, and a portion of the Hemlock-white pine-northern hardwoods forest region occurs south of it. This forest region extends westward from maritime Canada and northern New England, across southern Ontario and Quebec, to western Minnesota, and includes seven subdivisions characterized by forests of somewhat different composition, each of which occurs in distinct parts of the total region.

The Mixed mesophytic and the Oak-chestnut forest regions, as these are mapped by Miss Braun, closely approach western New York. The former extends from the Allegheny and Cumberland plateaus northward along the Allegheny River to the New York State border, while Oak-chestnut forest occurs across the east flank of the Appalachians to central Pennsylvania and northward to southern New England, with an extension up the Hudson River Valley.

Forests of the Erie-Ontario Lowland

The forests of the Beech-maple region in northwestern New York are imperfectly known. Although, as its name implies, *Fagus grandifolia* and *Acer saccharum* are the dominant trees throughout the entire forest region, many other species are present, and in the Erie-Ontario Lowland, oaks and hickories are particularly abundant. This suggests that the beech-maple area in western New York may not be solely an eastward extension of the deciduous forest of the Midwest, but that it may have affinity to the Oak-chestnut region of the eastern United States. This relationship has been emphasized by Bray (1915). It is also clearly depicted by Shantz and Zon (1924) who, in treating the vegetation of the United States, map what they call Chestnut-chestnut oak-yellow poplar forest throughout the lowland areas adjacent to Lakes Erie and Ontario in a wide band on either side of the Hudson River up to about Glens Falls and in most of the larger river valleys in the southern part of New York State. They represent these areas as northern extensions of oak forests of the same type which occur in broad areas on both sides of the Appalachians.

The only available detailed study of the vegetation of the deciduous forests of western New York (Shanks, 1966) deals specifically with Monroe County (see figure 1). However, its findings apply in general to other parts of the Erie-Ontario Lowland. Analysis of notes made by the first land surveyors and study of existing woodlots and original forest remnants permitted Shanks to prepare a map of the original vegetation of the county. Planimetric measurements of areas occupied by the vegetation types recognized shows the Beech-sugar maple type to account for 61 percent of the original vegetation cover. In order of decreasing areas, the remaining types were Hemlock-northern hardwoods (12 percent), Upland oak and Oak-hickory (11 percent), swamp forest (6 percent), Oak-chestnut-pine (4 percent), Mixed mesophytic (2 percent), and bog forest (2 percent). Today, in contrast, only 16 percent of the county is forested (Northeastern Forest Experiment Station, 1967).

Occurring on a wide variety of soil types, Beech-sugar maple forest covered more than half of Monroe County at the time of settlement. Both beech and sugar maple tend to maintain themselves at the better sites, and data are available which indicate that they succeed less mesophytic species. Typical beech-sugar maple stands exhibit abundant regeneration of the dominants. Sugar maple seedlings often form a continuous undergrowth, and beech root sprouts are generally abundant. Often codominant in forests of this type is *Tilia americana.* Other common associates include *Ulmus americana, Fraxinus americana, Ostrya virginiana, Acer rubrum, A. nigrum, Quercus rubra, Carya ovata, Prunus serotina,* and *Liriodendron tulipifera.*

Areas of Hemlock-northern hardwoods forest were originally found at the northeastern and northwestern corners of the county, mostly on the Lake Iroquois plain and in sheltered ravines near the Genesee River.

This forest type is dominated by *Tsuga canadensis, Fagus grandifolia,* and *Acer saccharum* which at places occur with *Betula alleghaniensis, Tilia americana, Acer rubrum, Fraxinus americana, Quercus rubra, Ostrya virginiana, Prunus serotina,* and *Ulmus americana.* Hemlock-northern hardwoods forests have a dense canopy, and light intensity on the forest floor typically is very low. Characteristic shrubs and herbs include *Acer pensylvanicum, Aster acuminatus, Dryopteris spinulosa* var. *intermedia, Lonicera canadensis, Lycopodium lucidulum, Maianthemum canadense, Sambucus pubens,* and *Taxus canadensis.*

The Oak-chestnut-pine type occurs on the driest sites which, in Monroe County, are underlain mostly by sandy deltas deposited in glacial lakes. An exact equivalent is probably not present westward across Genesee, Orleans and Niagara Counties for (although the three dominant oaks, *Quercus alba, Q. rubra,* and *Q. velutina* occur in these areas as does one of the dominant pines, *Pinus Strobus*) *P. rigida* is at present native no farther west than the vicinity of Rochester. There are no records of its occurrence westward in the State. Originally a member of this kind of forest, *Castanea dentata* has been eliminated as a canopy dominant by the chestnut blight.

Several other types of oak forest grow at slightly more mesophytic sites. The Upland oak type, in which *Quercus alba, Q. rubra,* and *Q. velutina* are the usual dominants, occurs on the tops and sides of drumlins and kames and on dry, flat-lying, gravelly soils of high porosity. *Carya ovata* is a frequent codominant and, at certain locations, additional species of *Carya* may attain dominance resulting in the Oak-hickory type. Transitional Oak-sugar maple associations occur at favorable locations between lowland Beech-sugar maple and Upland oak forests. Other transitional communities called Mixed mesophytic forests occupy positions between Oak-chestnut-pine and Hemlock-northern hardwoods types and, in some cases, in conjunction with Upland oak forests. Such transitional types, which generally are characterized by a large number of tree species occurring in about equal abundance, are of limited distribution in the county.

Large swamp forests were widely distributed in Monroe County and probably occupied about 6 percent of the total area. Deficient soil aeration is an important factor preventing invasion of the swamp habitats by more mesophytic species. In order of decreasing abundance, the following species occur in various combinations as dominants in different phases of the swamp forest: *Ulmus americana, Acer rubrum, A. saccharinum, Tilia americana, Fraxinus americana, Quercus bicolor, Fraxinus pennsylvanica,* and *F. nigra.*

Across the Erie-Ontario Lowland in forests of all types, Dutch elm disease has made serious inroads on *Ulmus* populations. The role of *U. americana* as a dominant or subdominant has ceased to exist over wide areas.

Forests of the Allegheny Plateau

The forest vegetation of the upland south of the Portage escarpment, as already noted, is mapped by Braun (1950) as part of the Hemlock-white pine-northern hardwoods forest region. More specifically, nearly all of southern New York and northern Pennsylvania is placed in the Allegheny Section of the Northern Appalachian Division which includes forests covering much of the northeastern United States and Canada south of the Gulf of St. Lawrence. It differs from the other major unit of the forest region, the Great Lakes-St. Lawrence Division, in the presence of *Picea rubens* which occurs at higher elevations throughout the mountains of the Northeast; in the absence of *Pinus Banksiana* and the rarity of *P. resinosa;* in the admixture of *Liriodendron tulipifera, Magnolia acuminata,* and other species characteristic of the central deciduous forest; and in the presence of certain herbs and shrubs including *Aster acuminatus, Tiarella cordifolia,* and *Viburnum alnifolium.*

The Hemlock-white pine-northern hardwoods region includes the Birch-beech-maple-hemlock (northeastern hardwoods) forest of Shantz and Zon (1924); the Beech-birch-maple forest type as it is recognized in Pennsylvania (Illick & Frontz, 1928); the Lake forest of Weaver and Clements (1938) the Maple-beech-birch forest type as it is applied by Armstrong and Bjorkbom (1956) to New York State; the Great Lakes-St. Lawrence forest region of Canada (Rowe, 1959); the Northern hardwoods region as identified in south-central New York State and north-central Pennsylvania (Goodlett & Lyford, 1963); the Northern hardwoods, the Northern hardwoods-fir, the Great Lakes pine, the Great Lakes and Northeastern spruce-fir, and the Conifer bog forests of Küchler (1964); and the Beech-birch-maple and White pine-hemlock-hardwood forest regions as applied throughout the northeastern United States by Lull (1968). Further equivalents and a review of the literature pertaining to the recognition of the Hemlock-white pine-northern hardwoods forest region are given by Nichols (1935).

The original forest cover of upland southwestern New York has been greatly modified by lumbering and

by clearing for agricultural purposes. However, because of low agricultural potential, upland counties have at present the largest areas of commercial and noncommercial forest land of any at the west end of the State (see table 2). Here, as elsewhere in western New York, an important stimulus for forest clearance during the early period of settlement was the demand for ashes which remained after burning cut trees. Crude field ashes were worth four to nine cents a bushel and, if the settler wished to refine these somewhat, 600 bushels could be leached and boiled down into a ton of pot or pearl ash (also called black salts) worth $125 to $150 (Munro, 1804; Young, 1875). Lye manufactured in this manner was used to make soap.

The nature and composition of the original forest is indicated by several virgin tracts preserved in northwestern Pennsylvania. These include the East Tionesta Creek Tract (Hough, 1936a) and Hearts Content (Lutz, 1930b) (both of which are in the Allegheny National Forest) and nearby Cook Forest (Morey, 1936). Hough and Forbes (1943) have summarized the numerous studies of forest remnants in this region.

Judging from early land survey records for a 175,000 acre tract in northwestern Pennsylvania (Lutz, 1930a), the forest existing today along the East Tionesta Creek is fairly typical of that which originally covered dissected areas of the Allegheny Plateau, particularly N-facing slopes. In both abundance and frequency values, *Tsuga canadensis* and *Fagus grandifolia* are the dominant canopy trees on plateau tops and on middle and lower slopes (Hough, 1936a). Third in order on middle and lower slopes is *Betula alleghaniensis,* but *Acer saccharum* holds this rank on plateau tops. In order of decreasing totals of abundance and frequency values, associated species are *Acer rubrum, Prunus serotina, Fraxinus americana, Liriodendron tulipifera, Magnolia acuminata,* and *Tilia americana. Viburnum alnifolium* is the most abundant shrub in forests of this kind and common herbaceous plants include *Dryopteris spinulosa, Lycopodium lucidulum, Maianthemum canadense, Mitchella repens, Oxalis montana,* and *Tiarella cordifolia.*

Within this type of forest, there is a tendency toward segregation of hemlock-beech, beech-hemlock-sugar maple, and beech-sugar maple communities, which differ from one another in the relative abundance of dominants. Hough (1936a) and Morey (1936) suggest that there is an alternation in the occupation of a given spot by hardwoods and hemlock-hardwoods. Uprooting or death of the hemlocks permits understory hardwoods to become established as canopy trees, while removal of canopy hardwoods, either catastrophically or by aging, allows hemlock seedlings to grow and dominate the canopy once again. In Cattaraugus County, forest of the Beech-sugar maple type originally occupied the better drained soils near ridge tops and was apparently more extensive in the glaciated portion of the plateau (Gordon, 1940). However, in this region today, most is of secondary origin, having developed after the removal of hemlock and white pine for lumber. *Fagus grandifolia* and *Acer saccharum* comprise 97 percent of the canopy in an undisturbed beech-sugar maple stand on a northeast slope in the Big Basin at Allegany State Park (Braun, 1950, Table 82).

White pine has an interesting position in the virgin forests of northwestern Pennsylvania. It is absent from the East Tionesta tract, but at Hearts Content, 30 mi to the west, it is abundant both in the hemlock and in the hemlock-beech communities. An age analysis shows the pine to have started as an even-aged stand at about 1680 (Lutz, 1930b). Similar data gathered at other localities on the Allegheny Plateau indicate that the presence of white pine can nearly always be correlated with fire, windfall, or some other event that opens a portion of the forest for seeding (Hough & Forbes, 1943). If no openings are made, the white pine apparently matures, dies, and is replaced by hemlocks or hardwoods, but not by other white pines.

Forest communities essentially the same as those in the Allegheny National Forest have been preserved at a few places in southwestern New York State, both outside and inside the glacial boundary. Gordon's map (1940) of the vegetation of Cattaraugus County at the time of settlement, which was prepared by analyzing the original lot survey data in conjunction with an examination of stands existing in the 1930's shows that the prevailing forest type in this area belonged to the Hemlock-white pine-northern hardwoods forest. Hemlock-northern hardwoods communities with little or no white pine comprised the typical stand. Quantitative data are unfortunately not available but a virgin tract of forest in Stoddard Hollow in the Big Basin at Allegany State Park has " a composition almost exactly similar to the Hemlock-Beech association at Heart's Content " (Gordon, 1937, p. 39). The principal trees on lower slopes in the Big Basin in order of decreasing abundance are *Fagus grandifolia, Tsuga canadensis, Acer saccharum,* and *A. rubrum* (Braun, 1950, Table 82). Together they total 87 percent of the canopy. The leading dominants in the Hemlock-beech association at Hearts Content are *Tsuga canadensis, Fagus grandifolia, Acer rubrum, Pinus Strobus,* and *Castanea dentata* in order of

decreasing totals of relative frequency and density for each species, recalculated in part from data provided by Lutz (1930b).

A number of other forest types are also recognized in Cattaraugus County (Gordon, 1940). As in Monroe County, drier sites which, in the upland, occur on ridges and exposed south and southwest slopes, were occupied by forest of the Oak-chestnut type. *Quercus alba, Q. rubra, Q. prinus,* and *Q. velutina* are now typically the dominant trees at these sites, but prior to about 1934, before being eliminated by the chestnut blight, *Castanea dentata* was codominant. Associated species, which sometimes reach dominant status, include *Pinus Strobus, Acer rubrum, Carya glabra, Betula alleghaniensis, Populus tremuloides,* and occasionally others. Similar communities also occur on dry S-facing slopes throughout northwestern Pennsylvania (Hough, 1936a). In Cattaraugus County, secondary forests rich in oak species commonly result after fires and excessive logging. Goodlett and Lyford (1963) have mapped the current extent of oak forest, using *Quercus alba* as an indicator species, to the east just beyond Allegany County. Species with frequencies greater than 50 percent in oak forests studied by these workers include *Quercus rubra, Q. alba, Acer rubrum, Pinus Strobus, Quercus velutina,* and *Q. Prinus.* Such forests occupy a greater area in this region than they do in western New York and Pennsylvania.

Communities transitional between the Oak-chestnut type of dry slopes and ridges and the Beech-sugar maple and Hemlock-beech types of the lower, more mesophytic sites are considered to be somewhat attenuated examples of Mixed mesophytic forests which occur across much of the southern part of the unglaciated Allegheny Plateau. Similar communities have been recognized at places in the Erie-Ontario Lowland associated with Upland oak forest (Shanks, 1966). Mixed mesophytic forests in Cattaraugus County occupy moist, well-drained, and well-aerated sites favorable to the growth of a wide variety of tree species. Such forests are dominated by *Quercus rubra, Fagus grandifolia, Acer rubrum, Betula alleghaniensis, Fraxinus americana, Prunus serotina* and, formerly, *Castanea dentata. Magnolia acuminata, Quercus alba, Liriodendron tulipifera, Pinus Strobus, Tilia americana, Carya cordiformis, Acer saccharum, Ostrya virginiana,* and *Acer pensylvanicum* can also occur.

Similar communities occur today in other areas of the upland. For example, in a stand near Lily Dale in Chautauqua County (Braun, 1950, table 85), the following trees comprised the canopy (in percent): *Tsuga canadensis* (20.9), *Fagus grandifolia* (16.9), *Prunus serotina* (12.4), *Acer rubrum* (11.3), *A. saccharum* (8.5), *Pinus Strobus* (8.5), *Magnolia acuminata* (5.7), *Quercus rubra* (5.6), *Fraxinus americana* (4.5), *Betula alleghaniensis* (2.8), *Tilia americana* (1.7), and *Carya ovata* (1.1). *Acer saccharum* accounted for 37 percent of trees in the second layer indicating potential for greater dominance by this species in the future.

Two additional forest types restricted to bottomlands have been recognized in Cattaraugus County (Gordon, 1940). The White pine-American elm forest occupied flood plains of the major rivers and streams in the county, especially those filled with impervious lacustrine sediments. The great value of *Pinus Strobus* as a timber tree led to the early destruction of these forests, but their former distribution has been well documented (*ibid.*). The largest area of this forest, occu-

TABLE 3

FOREST STAND DATA: GENERAL INFORMATION

Stand Name	Date Sampled	Soil Type	Drainage Class	Topography
Canadaway Creek	Sept. 1966	Volusia silt loam or Bath (Wooster) silt loam (Morrison *et al.*, 1919)*	well, or somewhat poorly	gently rolling, nearly flat-lying; lacustrine sediments (Muller, 1963)
Erie County Plantation #11	June 1966	Bath (Wooster) gravelly loam (Taylor *et al.*, 1929)	well	rolling, weak morainic topography
NYS Zoar Valley Property #12	Aug. 1966	Bath (Wooster) silt loam (Taylor *et al.*, 1929)	well	gentle NW-facing slope

* The topographic base on which this soil map was printed is apparently misdrawn in the vicinity of the stand as more recent maps show somewhat different relief and stream arrangement in the area. For this reason, it is impossible to determine which of the two soil types lay beneath the stand. A more recent soil association map for Chautauqua County shows the area covered by soils of the Langford-Erie Association, which contains soils very similar to those belonging to the Bath-Mardin-Volusia Association (Feuer *et al.*, 1955).

pying many hundreds of acres, occurred along the axis of the preglacial Allegheny River whose course ran toward Lake Erie from the northwest side of the Salamanca reentrant along what is today Conewango Creek (see Muller, 1963 for further details). These forests also contain *Fraxinus nigra, Quercus bicolor, Acer rubrum, Betula alleghaniensis, Tsuga canadensis,* and, occasionally, *Abies balsamea* and *Larix laricina.*

Of less widespread occurrence are the Bottomland hardwood forests which are found on recently deposited alluvium, especially along the Allegheny River and Cattaraugus Creek and their tributaries. These forests are variable in composition, but they are by no means as rich in numbers of species as the bottomland forests of Ohio and southern Michigan. *Populus deltoides, Salix nigra, Acer Negundo,* and *A. rubrum* are frequent along disturbed stream courses, while *Platanus occidentalis* and *Juglans cinerea* are found on the more stabilized flood plains.

Stands Sampled by the Point Quarter Method

During the summers of 1965 and 1966, the composition of some existing forest remnants in the upland around sites where cores for pollen analysis were collected was determined by studying 35 woodlots. The samples were scattered across southwestern New York State from western Chautauqua County to central Steuben County. Notes were taken on nearly all of the stands and three were sampled by the point quarter method (Cottam & Curtis, 1956) using an eight by six point grid in which the points were 20 m apart along the line of march. The presence of seedlings [6] over and under 30 cm tall and the presence of herbs was tallied by species within a meter-square quadrat centered over each of the 48 points. The area around each point was then divided into four quarters using the transect line as a bisect and a second line passed through the point at right angles to the bisect. Bamboo wands temporarily marked these lines. For each of the quarters, the distance between the point and the nearest tree, its species and diameter at breast height were recorded. The four trees were generally well beyond the original meter-square quadrat. Within an area one meter on each side, of a line between the points, the number of saplings of various species was tabulated.

The three stands were chosen because they met the following criteria: (1) size greater than 15 acres to reduce the influence of surrounding fields and secondary forests, (2) absence of disturbance in the form of fire, grazing, or excessive cutting (none or very little during the past 40 years), and (3) occurrence on upland soil types. The data for each stand were divided into four equal parts and a Chi-square test of homogeneity was applied to determine if the number of major tree species within any segment deviated significantly from the number expected on the basis of uniform distribution (Curtis & McIntosh, 1951). In no case did Chi-square values exceed the expected values at the 5 percent level, indicating that the stands were homogeneous according to this test.

The location of the stands in relation to the sites selected for palynological study is shown in figure 2. Other pertinent data concerning the stands are summarized in table 3. Relative frequency (percent frequency), density (percent occurrence), dominance (percent basal area), and the sum of these three figures (the importance value), in addition to the absolute density (number of trees/acre) and dominance (basal area/acre), were calculated for each species in the tree and sapling classes (Curtis, 1956). The relative frequency of seedling and herb species was also computed. These data are given in appendixes A through F.

Although too few in number to permit complete assessment of variability in existing forests of southwestern New York, the sampled stands nevertheless provide quantitative data on the composition of several upland communities. *Acer saccharum, Fagus grandifolia,* and *Tsuga canadensis,* in order of decreasing importance values, are the dominants in all three stands. High importance values for sugar maple, beech, and hemlock saplings indicate continued dominance by these species, although hemlock seedlings are less frequent than seedlings of the other two species. While quantitative data for comparison are not available, the three stands belong to the Hemlock-white pine-northern hardwood forest of Nichols (1935). This unit is recognized by Gordon (1937, 1940) to be the climatic climax of the entire upland in southwestern New York State where it is expressed by associations in which *Tsuga canadensis* occurs by itself or mixed with *Fagus grandifolia, Acer saccharum,* and *Betula alleghaniensis.* Although present in all three of the stands sampled, *Betula alleghaniensis* has uniformly low importance values. Since this species reproduces best at moist sites (Hough & Forbes, 1943), the three stands may not be edaphically suited to greater domination by yellow birch.

In Erie County Forestry Department Plantation #11 (appendix C), *Prunus serotina* has a relatively high im-

[6] Size classes follow Curtis (1959). *Trees* are greater than 4 in (ca. 10 cm) in diameter at breast height (d.b.h.); *saplings* are between 1 in (2 cm) and 4 in d.b.h., and *seedlings* are less than 1 in d.b.h.

portance value as a tree, but the sample includes no saplings. However, seedlings, mostly plants with cotyledons still attached, ranked second in frequency in the meter-square quadrats. These data accord well with the behavior of black cherry as it is known in the forests of northwestern Pennsylvania *(ibid.)*. Although black cherry seedling mortality is high in this region, a few always survive, growing slowly in moderate shade, and if logging, fires, or windthrow expose them to full sunlight, they are able to outgrow all important competitors. Several well-rotted stumps in Plantation #11 are evidence that selective cutting, perhaps as long ago as the turn of the century, may have been the factor which opened the stand enough to allow the establishment of *Prunus serotina* in the canopy.

The fourth and fifth most important tree in two of the stands is *Tilia americana,* but this species was not encountered while sampling the third. Judging by early land survey notes (Lutz, 1930a) and data published by Braun (1950), Gordon (1940), and Hough (1936a), basswood is a fairly consistent member of forests in various successional stages across the northern Allegheny Plateau. It is also a member of the mature forests in the East Tionesta Tract. White ash, *Fraxinus americana* occurs in all three sampled stands, but its importance values (in the tree class) are slightly lower than those for *Tilia.* Seedlings and saplings of *Fraxinus americana* are fairly abundant in the virgin forests of northwestern Pennsylvania, and while this species maintains itself there as well as *Betula alleghaniensis* does, *Fraxinus americana* is more successful in terms of persistence than *Prunus serotina* (Hough & Forbes, 1943).

Of the 16 herbs listed by Nichols (1935) as characteristic of the Hemlock-white pine-northern hardwood forest region, only the following appeared in quadrats in all three sampled stands: *Dryopteris spinulosa* var. *intermedia, Viola canadensis, V. incognita,* and *V. rotundifolia.* Others such as *Actaea pachypoda, Lycopodium lucidulum, Maianthemum canadense, Mitchella repens, Oxalis montana, Trillium erectum,* and *T. grandiflorum* were present in one or two of the stands, but eight additional species mentioned by Nichols were not encountered in any quadrats. A total of 49 species of herbs was recorded, although many other species were noted outside the quadrats. It is interesting that in all three stands at the time of sampling, *Arisaema triphyllum* and *Viola incognita* had the highest relative frequency values of herbaceous plants identified to species.

R Values

One assumption basic to using pollen analysis to investigate vegetation change is that a relationship exists between the number of pollen grains in a sediment sample and the abundance of the one or more species that produced this pollen in the vegetation surrounding the site of deposition. However, studies which have related pollen rain to contemporary vegetation demonstrate that the relationship is often not proportionate (Curtis, 1959; Davis & Goodlett, 1960; Janssen, 1967; McAndrews, 1966). Although some pollen types in surface samples apparently are represented accurately in relation to the abundance of the parent plants, others are either overrepresented or underrepresented. The causes of disproportionate representation are many, but most important are the great variability in pollen production by different species, the type of pollination and ease with which pollen dispersal takes place in wind pollinated species, and differential susceptibility of pollen to degradation by chemical and biological agents once deposition has taken place.

When interpreting fossil pollen assemblages, one way to compensate for disproportionate representation is to apply numerical correction factors based on the relationship between the percentage of one type of pollen in a sample and a quantitative abundance measure of the one or more species producing that type in the vegetation (Davis, 1963). Pollen percentages are available throughout a sediment column, but there is no known method of determining corresponding forest composition in other than two levels: (1) the surface pollen spectrum, where the vegetation can be directly sampled or its composition derived from published studies, and (2) the pollen spectrum immediately below the presettlement to postsettlement boundary where original survey records, which include quantitative data amenable to ecological analysis, can be used to estimate composition. It is the ratio between the pollen percentage of a given species and its vegetational percentage that provides a correction factor, or R value (*ibid.,* 1963), which, when divided into the number of pollen grains of that species as they are tallied by spectra along the sediment column, adjusts pollen counts to conform more closely to presumed abundance of species in the vegetation. Pollen types with R values <1 are underrepresented in sediments, those with values >1 are overrepresented, and those with values about 1 are proportionately represented.

At present, pollen of different species of *Betula, Carya, Quercus,* and *Ulmus* cannot be identified except,

in the case of *Betula,* by time consuming size-frequency measurements. Therefore, only generic level R values can be obtained for these taxa. Because other pollen types can be identified to species, however, R values for these apply to units which are of greater usefulness in ecological interpretation.

R Values From U.S. Forest Service Survey Statistics

The Northeastern Forest Experiment Station (1967) has published the most recent quantitative data on the present vegetation of southwestern New York State. This information was collected during a resurvey of the forest resources of the state undertaken to update an initial survey completed in 1952 (Armstrong & Bjorkbom, 1956) and to obtain an estimate of the total timber volume, total periodic tree growth, and other statistics of use principally to foresters and economic planners. The sampling design used in both surveys is fully described by Bickford *et al.* (1963).

Perhaps the most meaningful figures in the resurvey data for calculating R values are those of total volume by species on commercial forest land. To facilitate this computation, raw data listing commercial timber species 5 in and greater in diameter in millions of cubic feet have been recalculated as percentages. The percent total volume figures for species recognized in the survey are listed by county in table 4. The figure which pertains to a given species within the county where the bog is located was used in R value calculation.

Surface samples analyzed for pollen were collected at sites where sediment sampling was done. In each case, the sample taken was from a fairly dense but actively growing sphagnum polster and comprised the upper 1 to 2 cm from an area of about 10 cm². Two subsamples from each were macerated in the laboratory and their residues were ultimately combined and counted together. Inasmuch as about 50 percent of the total pollen in surface spectra is contributed by herbaceous plants, reflecting the large area of nonforest land in southwestern New York State (see table 2), counts were recalculated using the sum of arboreal pollen as the percentage base. This is necessary because the forest composition percentages are based on total forest land, not on land of all classes. R values calculated from these two sets of data are listed in table 7.

R Values From Original Lot Survey Data

The original land survey of western New York was privately sponsored, but was similar in organization to the rectangular pattern used in the General Land Office Survey of public lands west of the Appalachian Mountains. This system of surveying was authorized by Congress in 1785. Prior to this time metes and bounds, the establishment of property boundaries according to

TABLE 4

PERCENT TOTAL VOLUME OF TREES * ON COMMERCIAL FOREST LAND IN EIGHT WESTERN COUNTIES IN NEW YORK STATE †

Tree Species / County	Chautauqua	Cattaraugus	Allegany	Erie	Wyoming	Niagara	Genesee	Orleans
Acer saccharum	23.7	21.8	24.9	18.6	19.3	18.6	17.6	18.1
Fagus grandifolia	8.6	9.0	8.5	4.6	4.7	4.4	4.3	4.5
Tsuga canadensis	8.6	8.4	8.9	5.1	4.7	5.0	5.1	4.9
Betula alleghaniensis	1.0	1.2	1.0	1.8	1.7	1.7	1.8	1.4
B. lenta	1.1	1.3	1.0	0.5	0.4	0.6	0.4	0.3
Fraxinus americana	6.5	6.0	5.7	8.9	9.0	9.2	9.4	9.4
Tilia americana	3.8	4.0	3.6	8.0	8.3	8.6	7.8	7.6
Prunus serotina	3.4	3.6	3.3	3.9	3.8	3.9	3.9	4.2
Ulmus sp. or spp.	2.7	3.0	2.8	9.4	8.5	8.6	10.8	9.0
Acer rubrum	13.2	12.9	13.5	14.7	14.3	14.2	14.9	13.9
Quercus spp.	15.0	15.0	14.6	5.9	5.6	6.4	5.5	6.6
Carya spp.	2.1	2.4	2.0	5.6	5.7	5.6	5.3	5.9
Pinus Strobus	2.0	2.1	1.9	4.0	4.4	4.2	3.5	4.9
P. resinosa	3.7	3.6	3.5	2.1	3.2	2.5	1.8	2.8
Populus sp. or spp.	3.1	3.9	3.3	2.7	2.3	2.8	3.3	3.1
Misc.‡	1.6	1.8	1.5	4.4	4.0	3.9	4.7	3.5

* Commercial tree species 5 in in diameter or greater.

† Data from Table 11 in " Preliminary forest survey statistics by counties and units, New York — 1967," Northeastern Forest Experiment Station, U.S. Forest Service, Upper Darby, Pennsylvania.

‡ Includes other hardwoods and softwoods.

natural features, was practiced (Bourdo, 1956). In the rectangular survey of western New York a grid of north-south range and east-west township lines bounding townships generally 6 miles square was laid out west of a line extending north from central Allegany County through eastern Wyoming, Genesee, and Orleans Counties, the area encompassed by the Holland Purchase (Evans, 1924; Turner, 1850). The number of townships per range varied from 16 in the eastern ranges to three in far western Chautauqua County. These townships have only partly retained their identity as political units in contrast to those in the region surveyed by the rectangular method to the west.

The surveying of township and range lines began under the direction of Joseph Ellicott in the spring of 1798, shortly after the Holland Land Company acquired clear title to western New York, and continued until 1800. The internal survey of townships into lots was largely completed by 1810 but a few of the townships in southern Cattaraugus County were not divided until 1819. It was the custom in the Ellicott survey to mark each lot corner with a post. Records were kept of the direction, diameter, and species of from one to four bearing-trees located in different quarters surrounding the post. Since land sale was of paramount concern, Ellicott directed his surveyors to take careful notes on the topography, soils, timber, windfalls, springs, and other natural features along the survey lines. When running a lot line the surveyors made a list of the predominant timber encountered and, if the forest composition varied along a lot line, several lists were recorded. It is perhaps reasonable to assume that species listed were arranged in order of decreasing abundance, as they were in the General Land Office surveys, but no evidence exists that this was the case.[7]

Lot survey data [8] for the region around the sites where the presettlement to postsettlement boundary is preserved in the pollen record have been compiled. Estimates vary as to the area which contributes to the pollen rain accumulating at a given point. Faegri and Iversen (1964) consider that in forested regions pollen is not transported in significant quantities for more than 50 km (ca. 30 mi), while Tauber (1967) mentions much shorter distances. Data for an area, seven lots by seven lots (ca. 30 mi^2), was used around Allenberg and Houghton bogs. The area of study around Protection Bog had to be restricted to a tract of 16 mi^2, however, because the notes for western Wyoming County could not be located. Examination of additional data beyond the included lots suggests that the basic data would not be altered greatly by enlarging the areas investigated except that more species of infrequent mention would appear.

The data collected were analyzed in two ways. Since the bearing-trees recorded by the surveyors represent a low density sample of the forest within each of the three areas, the relative frequency, relative density, and relative dominance of each species noted can be calculated following the methods used in treating the forest stands discussed earlier. The sum of these three measures, or the Importance Value, for all the species within one area totals 300, but for purposes of R value computation, the percent total for each of the species, or an importance percentage (McAndrews, 1966), was calculated. Trees mentioned along lot lines were treated in a different manner. For each area the total number of times a given species was mentioned was tallied and this sum was rendered as a percentage of the total trees of all kinds mentioned throughout the area. Percentages from both kinds of data were used as denominators for R value calculation. Pollen percentages used as numerators in the ratios were provided by the first spectrum immediately below the presettlement to postsettlement boundary which is clearly marked by a sharp increase in the pollen of *Ambrosia, Plantago,* and other genera associated with forest clearance. The percentage

[7] The richness of data included in the Ellicott survey is illustrated by notes pertaining to Lot 60, T. 9 R. 5 (southeastern Erie County) extracted from field books kept at the Erie County Clerk's Office, Buffalo, New York.

The boundary line of this lot begins at a beech post marking the northeast corner and passes westward across an upland of the first quality timbered with beech (*Fagus grandifolia*), hemlock (*Tsuga canadensis*), bass (*Tilia americana*), and elm (*Ulmus* sp.) to an upland of the second quality, then across a deep gully and abruptly back again to an upland of the first quality with hemlock, beech, and sugar maple (*Acer saccharum*) timber, and finally to a beech post at the northwest lot corner. Southward from this point the line passes through land considered excellent for meadow and timbered with sugar maple, cherry (*Prunus serotina*), bass, and elm, to a sugar maple post at the southwest corner of the lot. A short distance to the east of the post, the line descends into an intervale of the first quality timbered with buttonwood (*Platanus occidentalis*), elm, white ash (*Fraxinus americana*), and bass, crosses a stream, and rises onto an upland of the first quality. It then crosses two adjacent streams separated by land with hemlock and beech timber, from where it passes through a sugar maple stand on upland of second quality with yellow loam soil to a beech post at the southeast corner of the lot. Northward, returning to the point of origin, the line extends through land broken by deep gullies and covered with hemlock, beech, and sugar maple timber. The surveyor listed seven bearing-trees, two at each of three posts, and one at the fourth. One of these was a hemlock 8 in in diameter; the remaining six were beeches, 6, 7, 8, 12, 24, and 30 in in diameter.

[8] Notes for Houghton and Protection Bog areas are kept by the Erie County Clerk. Both areas were surveyed by Cotton Fletcher in 1807 and 1808. Notes pertaining to the Allenberg Bog area are on file with the Cattaraugus County Clerk, County Building, Little Valley, New York. Also available for this county are plat maps on which bearing-trees are noted at lot corners. I have been unable to determine who made the survey.

base used in this calculation includes both arboreal and nonarboreal pollen types because the latter were only sparsely represented and did not greatly reduce percentages of tree pollen types.

In all three areas, *Fagus grandifolia* accounts for 50 to 75 percent of the sum of bearing-tree importance values (see table 5). *Acer saccharum* is consistently second in importance. *Tsuga canadensis* and *Betula alleghaniensis* rank third and fourth in the Houghton and Protection Bog areas and sixth and fifth around Allenberg Bog. About the same arrangement of species occurs in the frequency of mention values which are listed in decreasing order in table 6. *Fagus grandifolia* is the most frequently mentioned tree, followed by *Acer saccharum. Tsuga canadensis* shares the third position with *Tilia americana* around Allenberg Bog; it ranks fourth around Houghton Bog, being preceded by *Tilia americana,* and third around Protection Bog where *T. americana* directly follows it in importance. In most cases the three species with the highest bearing-tree importance and frequency of mention values in the survey data are also the three leading species in the data from the stands studied by the point quarter method.

Both estimates of presettlement forest composition may be biased. *Fagus grandifolia* was by far the commonest bearing-tree, but whether beech was indeed the dominant tree in the forest around the bogs might be questioned. Presumably, surveyors selected trees closest to the lot corner irrespective of species, but because beech has a light colored, easily marked bark and is of lesser value as a timber tree, they may have chosen it as a bearing-tree over other species. Noting the preponderance of beech bearing-trees throughout Cattaraugus County, Gordon (1940) has concluded, however, that in spite of possible bias, beech was probably the most common tree in the original forest, a conclusion substantiated by the high percentage of beech pollen in presettlement spectra. *Tilia americana* was not used at all as a bearing-tree, although it had a fairly high rank in the frequency of mention data. This discrepancy perhaps can be explained because *Tilia* is not a long-lived, rot-resistant tree and is therefore not entirely suitable as a bearing tree. Its high position in the frequency of mention data may be in part a reflection of its value as an easily worked wood often employed in pioneer carpentry.

Discussion of R Values

The three sets of R values from the different bog areas are compared in table 7. Although ratios for certain pollen taxa are fairly consistent, others vary widely. The best example of the latter group is *Pinus* spp. whose values range from about 1 to 5 using the modern data and from 7 to 57 using the presettlement data. These figures, and particularly the ones derived from the presettlement data, emphasize pine pollen's typical overrepresentation. However, one difficulty in using surface sample pollen percentages to obtain R values representative of pine as it occurs in natural forests is that both native and exotic species now grow and contribute to the pollen rain in western New York. Thus pollen dispersal capacity of pines of both types influences surface counts. Since only native species are represented in presettlement spectra, the R values obtained from surface spectra cannot be applied indiscriminately throughout postglacial time. Another problem is that locally growing reforested pine stands may contribute more pollen to surface spectra than is typical of the region from which the vegetation composition data were derived. An R value of 5.0 at Protection Bog probably reflects the influence of several nearby mature, planted *Pinus resinosa* and *P. Strobus* stands. That local overrepresentation is indeed operative at this site is substantiated by the sharp decrease in *Pinus* subg. Pinus (*diploxylon* type) and *P.* subg. *Strobus* (*haploxylon* type) pollen percentages in the upper 5 cm of sediments. Pollen below this depth accumulated before the plantations existed.

R values for *Ulmus* spp. are also variable but to a lesser degree. They range from 0.5 to about 5.0, but most values are over 1.0, implying overrepresentation. Similarly, overrepresentation is indicated for *Quercus* spp. The R values for this pollen type calculated from the modern data suggest that the oaks are somewhat less than twice overrepresented, while the only presettlement value implies that they are nearly 13 times overrepresented. Little emphasis should be given to this one presettlement value, however, because of the rather small area used to obtain the percentage of oaks in the vegetation. Since *Quercus* pollen seems to be transported for fairly long distances, a much larger area should perhaps be sampled to gain an accurate estimation of the abundance of oak trees contributing to the pollen rain. In northern Vermont where *Quercus rubra* is the principal pollen-producing oak, Davis and Goodlett (1960) have found oak pollen to be the most overrepresented of all pollen types in their spectra. R values for *Tsuga*, with one exception, are fairly constant and imply that *Tsuga* pollen is also somewhat overrepresented. My figures compare fairly well with those calculated for hemlock in northern Vermont (*ibid.*), but differ from the correction factor for the species used

TABLE 5

Presettlement Survey Data: Relative Frequency, Relative Density, Relative Dominance, Importance Values, and Importance Percentages of Bearing-Trees used in the Original Lot Survey of the Areas Around Allenberg, Houghton, and Protection Bogs

Tree Species and Bog Area	Relative Frequency	Relative Density	Relative Dominance	Importance Value	Importance Percentage
Fagus grandifolia					
Allenberg Bog area	70.1%	86.5%	84.1%	240.7	80.2
Houghton Bog area	65.2%	74.7%	71.4%	211.3	70.4
Protection Bog area	53.8%	62.3%	47.9%	164.0	54.7
Acer saccharum					
Allenberg Bog area	17.2%	8.7%	8.1%	34.0	11.3
Houghton Bog area	16.7%	12.1%	11.8%	40.6	13.5
Protection Bog area	26.2%	21.7%	22.2%	70.1	23.4
Tsuga canadensis					
Allenberg Bog area	1.2%	0.4%	1.4%	3.0	1.0
Houghton Bog area	7.6%	5.1%	9.8%	22.5	7.5
Protection Bog area	7.7%	6.6%	14.9%	29.2	9.7
Betula alleghaniensis					
Allenberg Bog area	2.3%	0.9%	2.3%	5.5	1.8
Houghton Bog area	3.0%	2.0%	2.1%	7.1	2.4
Protection Bog area	4.6%	2.8%	5.2%	12.6	4.2
Prunus serotina					
Allenberg Bog area	2.3%	0.9%	3.2%	6.4	2.1
Houghton Bog area	3.0%	3.0%	1.1%	7.1	2.4
Protection Bog area	—	—	—	—	—
Acer rubrum					
Allenberg Bog area	—	—	—	—	—
Houghton Bog area	—	—	—	—	—
Protection Bog area	3.1%	2.8%	5.8%	11.7	3.9
Ulmus sp.					
Allenberg Bog area	—	—	—	—	—
Houghton Bog area	3.0%	2.0%	2.1%	7.1	2.4
Protection Bog area	1.5%	0.9%	1.0%	3.4	1.1
Carpinus/Ostrya					
Allenberg Bog area	4.6%	1.7%	0.4%	6.7	2.2
Houghton Bog area	—	—	—	—	—
Protection Bog area	1.5%	0.9%	0.2%	2.6	0.9
Fraxinus americana					
Allenberg Bog area	1.2%	0.4%	0.4%	2.0	0.7
Houghton Bog area	—	—	—	—	—
Protection Bog area	1.5%	1.9%	2.9%	6.3	2.1
Pinus Strobus					
Allenberg Bog area	—	—	—	—	—
Houghton Bog area	1.5%	1.0%	1.7%	4.2	1.4
Protection Bog area	—	—	—	—	—
Juglans cinerea					
Allenberg Bog area	1.2%	0.4%	0.1%	1.7	0.3
Houghton Bog area	—	—	—	—	—
Protection Bog area	—	—	—	—	—

TABLE 6

Presettlement Survey Data: Frequency of Mention of Tree Species Along Lot Survey Lines for Areas Around Allenberg,* Houghton,* and Protection† Bogs

Tree Species	Allenberg Bog Area	Houghton Bog Area	Protection Bog Area
Fagus grandifolia	30.6%	30.0%	28.2%
Acer saccharum	22.1%	24.3%	17.3%
Tsuga canadensis	14.6%	11.1%	19.7%
Tilia americana	14.6%	13.0%	14.6%
Ulmus sp.	5.1%	6.2%	3.2%
Betula sp.	1.6%	3.2%	5.1%
Fraxinus americana	1.4%	5.4%	2.9%
F. nigra	1.0%	2.5%	3.9%
Acer rubrum	0.4%	0.5%	3.2%
Magnolia acuminata	1.8%	0.2%	0.7%
Prunus serotina	0.2%	2.1%	0.2%
Alnus sp.	1.4%	0.8%	0.2%
Castanea dentata	2.4%	——	——
Quercus rubra and/or *velutina*	1.0%	——	——
Juglans cinerea	——	0.3%	0.5%
Pinus Strobus	0.2%	0.3%	0.2%
Picea mariana	0.4%	0.2%	——
Abies balsamea	0.4%	——	——
Larix laricina	0.4%	——	——
Quercus alba	0.2%	——	——

* Area equal to 17,640 acres.
† Area equal to 10,080 acres.

in Wisconsin by Curtis (1959) who has multiplied numbers of hemlock pollen in fossil spectra by three to obtain proportional representation. Since R values differ from one major geographic region to another (see Comanor, 1968), the use of one correction factor over a wide area is inappropriate.

The R values for *Betula* spp., using both modern and presettlement data, indicate that it is greatly overrepresented, a finding that substantiates the studies in Vermont and Wisconsin cited above. Although I cannot be certain which species of birch produced a given pollen grain, it is likely that only two species, *Betula lenta* and *B. alleghaniensis*, contributed most of the birch pollen to the spectra because the other species reported from western New York, *B. papyrifera* and *B. pumila*, are rare in this region and occur mainly in the Erie-Ontario Lowland (Zenkert, 1934).

According to my data, only *Fagus grandifolia* and *Juglans cinerea* are proportionately represented. To these may be added *Carpinus-Ostrya* if the average of the two R values in the table is taken to be meaningful. The pollen of *Carpinus caroliniana* and *Ostrya virginiana* is morphologically very similar, so no attempt was made to tally these species separately. Since their autecology differs and the abundance of *Carpinus* in the vegetation is unknown, significance cannot be given to R values for this pollen type. Davis and Goodlett

TABLE 7

R VALUES CALCULATED USING VARIOUS ESTIMATES OF VEGETATION COMPOSITION

R values	Allenberg Bog			Houghton Bog			Protection Bog		
		Presettlement			Presettlement			Presettlement	
Pollen taxa	Modern	Importance % age	Freq. of mention	Modern	Importance % age	Freq. of mention	Modern	Importance % age	Freq. of mention
Pinus spp.	1.04	——	56.50	1.61	7.14	33.33	5.00	——*	38.00
Tsuga canadensis	1.40	23.60	1.62	2.08	2.81	1.90	1.33	2.53	1.24
Betula spp.	9.92†	8.61	9.69	10.26†	5.67	4.25	7.43†	2.43	2.00
Fagus grandifolia	0.70	0.22	0.58	1.37	0.36	0.85	1.48	0.42	0.82
Quercus spp.	0.97	——*	12.83	1.83	——*	——*	1.90	——*	——*
Acer saccharum	0.55	0.46	0.24	0.67	0.52	0.28	0.42	0.34	0.49
A. rubrum	0.22	——*	1.00	0.13	——‡	——‡	0.06	——‡	0.25
Carya spp.	0.79	——*	——*	0.25	——*	——*	0.23	——*	——*
Ulmus spp.	2.56	——*	0.57	1.23	1.38	0.53	0.53	4.73	1.63
Tilia americana	0.03	——*	0.03	0.03	——*	0.02	0.01	——*	0.07
Fraxinus									
4-colpate	0.22	0.57	0.29	0.11	——*	0.15§	0.17	1.00§	0.48
3-colpate	——	——*	0.70	——‖	——*	——*	——‖	——*	0.18
Populus spp.	0.38	——*	——*	0.74	——*	——*	0.81	——*	——*
Carpinus/Ostrya	——‖	0.23	——*	——*	——*	——*	——‖	2.11	——*
Juglans cinerea	——‖	0.67	——*	——*	——*	1.00	——‖	——*	——*
Castanea dentata	——‖	——*	0.29	——*	——*	——*	——‖	——*	——*

* Not present in presettlement vegetation data; † Forest survey percentages of *Betula lenta* lumped with *B. alleghaniensis;* ‡ Lumped with *Acer saccharum;* § Includes *Fraxinus* 3-colpate; ‖ No forest survey statistics available.

(1960) found the basal area percentage of *Ostrya virginiana* in a forest in northern Vermont to be nearly equal to the percentage of its pollen in surficial pond sediments. These authors have also found *Fagus grandifolia* to be ± proportionately represented, although the percentage of beech pollen in their surface sediment was slightly greater than the percentage of beech in the surrounding forest.

Acer rubrum, A. saccharum, Carya spp., *Castanea dentata, Fraxinus* 4-colpate (incl. *F. americana* and *F. pennsylvanica*), *F.* 3-colpate (*F. nigra*), *Populus* spp., and *Tilia americana* are underrepresented. Also in this category, although not listed in table 7, is *Prunus serotina*, a species which apparently is entirely insect-pollinated because its pollen was not found in any of the spectra analyzed even though black cherry did occur in the surrounding forest. The low values for *Tilia* and *Acer* species may likewise reflect the influence of insect pollen vectors.

Sangster and Dale (1964) have emphasized an additional reason for underrepresentation. They demonstrate that pollen of different species vary in their resistance to degradation, implying that species of low resistance will be underrepresented regardless of the amount of pollen they produce or the effectiveness of its dispersal. Working mostly with species native to eastern North America, these authors have experimentally shown *Acer saccharinum* and *A. saccharum* pollen to be less well preserved in peat than the pollen of species of *Betula, Fraxinus, Pinus, Quercus,* and *Ulmus,* and that *Populus tremuloides* pollen is the most severely degraded of all types investigated.

Similar results pertaining to *Populus* are implied in data from New York State. At the four stations in the southwestern corner of the state where airborne pollen data have been collected (Ogden & Lewis, 1960), *Populus* pollen is well represented, exceeding *Pinus* in numbers of grains per cm^2 of slide surface, and occasionally equalling such other heavy producers as *Quercus* and *Ulmus*. Similar counts do not occur in samples analyzed from bog surfaces. This may reflect both the ease and the speed with which *Populus* pollen is decomposed. Sangster and Dale in an earlier study (1961) show that 80 percent of fresh poplar pollen samples placed at the surface of a peat bog was degraded within 32 days.

Perhaps the most significant set of R values from the standpoint of the accuracy of the method used to estimate vegetation composition is that calculated from the Forest Service survey statistics. Since the three sites where the current pollen rain was determined are relatively close together and have more or less similar surface pollen spectra, one way to summarize R values of pollen taxa included in table 7 is to compute an average value for each. Arranged in decreasing magnitude and placed in the three classes of representation, these are: (1) overrepresentation—*Betula* spp., *Pinus* spp., *Tsuga canadensis, Quercus* spp., and *Ulmus* spp.; (2) proportional representation — *Fagus grandifolia*; and (3) underrepresentation — *Populus* spp., *Acer saccharum, Carya* spp., *Fraxinus americana* and/or *pennsylvanica, Acer rubrum,* and *Tilia americana.*

The Pollen Diagrams

(see page 102)

METHODS

Field Techniques

The four basins selected for palynological study (see figure 2) appear to be ice-block depressions. Protection and Houghton bogs are associated with the Valley Heads moraine and were chosen because their proximity permits regionally-significant trends to be determined in the pollen profiles. Parallel trends duplicated at many sites throughout a region are more important in reconstructing the pattern of vegetation change than smaller, short-term changes present at only one site. The two other deposits are located south of the Valley Heads moraine on drift deposited at an earlier time. Allenberg Bog is near the terminal position of the Kent moraine, and the Genesee Valley Peat Works is on a still older surface, apparently of Olean age.

At each site along a series of compass-oriented transects, sediment lithology and depths were determined with a Davis sampler (Eberbach, Ann Arbor, Michigan). As three of the four sites lack a central bog lake, traverses were easily made across the semi-firm bog surface. At the fourth site, a series of soundings around the mat at the edge of a small lake 50 m in diameter was made. The goal in all cases was to find the deepest spot in the basin at which samples for pollen analysis could be collected. At two of the sites, the upper sediments were too watery to be sampled with the equipment used so a supplementary sample series was taken in the firmer sediments to one side of the main sampling point.

Three standard samplers were available and these were employed depending on the nature of the sediments encountered. At most sites a Hiller sampler (Borros, Solna, Sweden) with a 50 cm chamber was used. This instrument worked best in coarse, fibrous peat of variable compactness, in finer peat deposited from water, and in the stiffer lake muds or gyttjas. Lake sediment was also collected with a Livingstone piston corer of the style described by Cushing and Wright (1965). An adapter, which allowed the sturdy Livingstone rods to be coupled to the head of the Davis sampler, was found to be particularly effective in penetrating heavier clayey sediments.

At Protection Bog, two samples for radiocarbon analysis were obtained with the Livingstone piston corer, equipped with a 2-inch barrel, from a location 50 cm to one side of the point where samples were taken for pollen analysis. Subsamples 10 cm in length were removed from the cores and submitted to Isotopes, Inc. for age determination. To check the location of the dated sediments in reference to the pollen diagram at this site, the pollen content of sediments immediately above and below the 10 cm segments was determined. These spectra match well those expected on the basis of depth alone (cf. diagram 1 and appendix G). The uppermost date at Protection Bog was based on peat collected with a specially made sampler, 4 in in diameter, built after the principle of the Livingstone piston corer. The bottom 10 cm of wet peat from the core was submitted for age determination.

The Houghton Bog date was obtained from wood which lodged in the Davis sampler during an exploratory probe of the area adjacent to the site where samples for pollen analysis were taken. An insufficient amount of wood was collected to permit both C-14 analysis and microscopic study, so identification was not attempted.

Extreme care was taken not to contaminate the samples collected for pollen analysis. When using the Hiller sampler, successively deeper samples 50 cm long were collected alternately from two holes 50 cm apart. The outer several millimeters of sediment uncovered by turning the outer sleeve to open the sediment chamber were cut away and discarded. The sediments thus exposed were removed with a micro-spatula from points midway between lines 5 cm apart stamped on the sampler head.

Individual samples were placed in pint polyethylene bags labeled with appropriate data. Cores collected with the Livingstone sampler were extruded in the field, wrapped in aluminum foil, labeled, and placed in plywood core boxes. Cores taken with the Davis sampler were also wrapped in foil and labeled in the field. Subdivision of the cores was done in the laboratory. All samplers were washed with clean water after each use. The sediment samples were refrigerated until macerated in the laboratory.

Laboratory Techniques

The standard methods for separating and concentrating pollen from sediments by removing inorganic and unwanted organic material were used in the preparation of the samples. A 1 cc subsample, measured with a glass graduated cylinder cut down to hold 1 $\pm$ 0.05 ml of water, was macerated in each case. The schedule employed during the maceration procedure depended on the type of sediment being analyzed.

Two main types of organic sediment were encountered. Pollen in peat was concentrated by following successively the steps detailed below:

(1) Place sample in 40 ml tapered centrifuge tube, cover with 10 percent KOH, and heat for 5 min in boiling water bath;
(2) Wash sample through #60 mesh sieve (250 μ) with enough distilled water to stop the KOH reaction (use sieve residue for identifying plants making up the peat);
(3) Centrifuge and decant; and
(4) Glacial HAc wash, acetolysis solution (Erdtman, 1960) in boiling water bath for 3 minutes, and glacial HAc wash.

Since gyttja, the other main kind of organic sediment found generally does not deflocculate in KOH, a partial breakdown of this sediment was accomplished using cold 10 percent HCl. The sediment was gently teased apart with a glass rod. After centrifuging and decanting the HCl, the sample was acetolyzed. If deflocculation had not completely taken place, the sample was heated for 5 minutes in 10 percent KOH in a boiling water bath. KOH was removed from the residue by centrifugation and distilled water washes.

Inorganic sediments containing calcium carbonate were treated first with 10 percent HCl, then acetolyzed, and, if necessary, finally treated with 10 percent KOH. Silty and clayey samples were exposed to cold, 72 percent HF for 24 hours culminated by an additional 30 minutes in a boiling water bath. After removal of HF by centrifuging and decanting, 10 percent HCl was added to the residue and the mixture heated in a boiling water bath for 3 minutes to dissolve colloidal silicon dioxide and silicon-fluorides. Residual acids were thoroughly washed from the organic residue with distilled water. Acetolysis, and in some cases exposure to 10 percent KOH, completed the maceration. If heavy minerals such as pyrite were present, heavy liquid separation (with zinc chloride, sp. gr. 1.93) immediately followed HF treatment.

After maceration, all residues were washed successively in distilled water, 96 and 100 percent ethyl alcohol, stained with 2–4 drops of safranin-0 in 100 percent ethyl alcohol, given a final 100 percent ethyl alcohol wash, and pipetted into labeled 3 dr vials. The staining was best if the residues soaked for 24 hours in distilled water prior to alcohol dehydration. Residues were stored in vials at room temperature until mounted for counting.

The technique used in mounting residues for microscopic study was devised to enable the calculation of the number of pollen grains per unit volume of sediment and is an adaptation of the method described by Davis (1965a, 1966). The residue was washed into a 12 ml graduated centrifuge tube with tertiary butyl alcohol (TBA) and brought to a known volume. After thoroughly mixing residue and TBA by vigorous pumping with a large bulb pipette, a certain volume of the mixture was removed from the tube with the pipette and from 3 to 15 drops were released onto a small amount of silicone oil (2000 cs) placed at the center of a slide on a slide warming table (ca. 75° C). Heat from the warming table rapidly evaporated the TBA leaving a mixture of silicone oil and residue.

To produce an even distribution of pollen grains under the cover slip, a dissecting needle was used to blend the pollen and the silicone oil. The needle was wiped clean on the underside of the cover slip, which was placed promptly downward over the preparation. After making three slides from each residue, TBA was removed from what remained of the residue with a 100 percent ethyl alcohol wash and the residue-ethyl alcohol mixture was pipetted back into the appropriate vials. It is necessary to carry out these procedures in a fume hood because of the noxious character of vaporized TBA. The volume of TBA-residue mixture in the graduated centrifuge tube and the number of drops of this used to make each slide were recorded.

Since the same pipette was used to mount every residue, the volume of one drop delivered by this pipette was more or less constant for all preparations. It was found, after 20 trials, that the pipette delivered 48.95 drops per ml. When counting, the number of traverses completed across a cover slip was recorded. Since in most cases the basic sum was reached before the entire area was examined, the following equation was used to determine the total number of pollen and spores under a cover slip: number of traverses / total number of possible traverses = sum of terrestrial pollen and spores / x, where x is the number of grains per slide or per y drops of residue-TBA mixture. Multiplying x by a factor, z ml of residue-TBA mixture in the centrifuge

tube · 48.95 / y drops delivered to the slide, gives the number of grains per ml of wet sediment.

Although many potential sources of error are present in this technique, it is considered to give reasonably reliable results for the amount of time expended. To test the accuracy of the mounting technique, the number of arboreal pollen grains for an equal number of traverses in each of two or three slides prepared from the same residue was determined. These data, listed in table 8, show that the method delivers similar numbers of pollen grains to individual slides in a series.

TABLE 8

DATA FOR CHECK ON MOUNTING TECHNIQUE USED IN THE DETERMINATION OF ABSOLUTE POLLEN FREQUENCY

Sample Number	Number AP	Number of Traverses *
Pb 7020–1	262	22
Pb 7020–2	236	22
Pb 7156–1	116	44
Pb 7156–2	117	44
Pb 7156–3	122	44
Pb 7157–1	264	44
Pb 7157–2	261	44
Pb 7180–1	266	22
Pb 7180–2	272	22
Pb 7906–1	159	44
Pb 7906–2	156	44
Pb 7906–3	160	44
Pb 7907–1	188	44
Pb 7907–2	185	44
Pb 7907–3	207	44

* Using a magnification of 250 diameters, 44 traverses are generally possible with little or no overlap across a 22 mm^2 cover slip.

One serious cause of error develops when the residue becomes concentrated under some sector of the cover slip. If, for example, pollen counts were made only in a zone of high concentration, fewer traverses would be necessary to reach a given sum than if the residue were evenly dispersed under the whole cover slip area. In this case, the calculated estimate of the number of grains per unit volume would be greater than was actually true. Visual inspection and adjustment in the location of the traverses was used to overcome this potential source of error. In most cases parts of several slides were also counted to obtain a representative sample of the residue.

Counts were uniformly made using equispaced traverses controlled by a calibrated mechanical stage. Distance between the traverses was initially chosen with reference to the density of the pollen under the cover slip. At low density, traverses were made closer together. Counting was done routinely at a magnification of 250 diameters using a Leitz Ortholux microscope. Grains difficult to identify were examined using a 95 X apochromatic oil immersion lens. As an aid to identification of pollen encountered in the preparations, a large collection of reference slides was assembled and the standard pollen identification manuals were frequently used (Erdtman, 1943, 1957, 1965, 1966; Faegri & Iversen, 1964; Wodehouse, 1935).

At least 500 pollen grains of trees were counted in nearly all samples. The percentage base used to calculate the relative pollen frequencies at a given level is the sum of arboreal pollen (AP) and nonarboreal pollen (NAP) at that level (spores and pollen of aquatics and bog plants were excluded), as this figure best represents the regional upland pollen rain (Wright & Patten, 1963). The percentage base varied from spectrum to spectrum with the greatest differences occurring in the uppermost postsettlement and in the basal inorganic sediments where NAP is abundant. Relative frequencies of other pollen taxa, mostly bog plants, aquatics, and pteridophytes, were calculated using as a new percentage base the sum of the first percentage base and the total number of pollen and spores of the miscellaneous taxa at a given level.

Pollen grains and spores which were well preserved but which could not be identified due to inadequacies in the pollen reference collection were classified as unfamiliar. Grains in the unknown category were in part corroded or broken, in part obscured by debris, and in other ways rendered indeterminable.

SITES ASSOCIATED WITH THE VALLEY HEADS MORAINE

Protection Bog

This basin is a large, fairly shallow, ice-block kettle now nearly completely filled with sediment. Peat comprises the upper 3 to 4 m, and the bog plant communities which currently occupy the surface continue to add to the deposit. The kettle occurs at an elevation of 1410 ft in an area of morainic topography of Valley Heads age somewhat north of the head of the Chaffee outwash plain. To the east, north, and west, the surrounding hills rise 300 to 400 ft. The bog is located in the Town of Holland near the southeast corner of Erie County, 0.2 mi west of the Erie-Wyoming County line, 1.8 mi northeast of Protection at 42° 37′ 20″ N. lat. and 78° 28′ W. long. It is shown as a wooded marsh in the northwest sector of the Arcade 7½′ quadrangle. The bog and much of the surrounding land is currently

Figure 4

owned by the County of Erie whose Bureau of Forestry administers the area as Plantation #5.

The bog surface is covered with vegetation (figure 4), and there is no standing water except for a temporary lagg along the north edge of the mat. As measured by planimetry on an aerial photograph, the original lake occupied an area of about 22 acres. Of this, 15 acres are now nonforested and covered mainly by ericaceous shrubs with occasional clumps of tamaracks. The basin has an irregular outline with the long axis trending east-west. There is a prominent bay extending northward, and smaller bays, which are now covered with deciduous swamp forest, occur at the east and west ends of the basin. The steepest slopes above the basin are found on the north and south sides. An intermittent shallow stream occurs at the east end, but the basin has no permanent outlet or inlet. The stream which discharges into a tributary of Buffalo Creek apparently functions only at the peak of spring runoff as it is nearly dry during the summer.

In spite of the advanced stage of basin infilling, most of the major vegetation zones characteristic of bog succession are still evident. On the north, east, and west sides occurs a prominent, almost impenetrable, high shrub zone composed of *Vaccinium corymbosum, Pyrus melanocarpa,* and *Nemopanthus mucronata. Rhododendron nudiflorum* is also present but is less frequent. The western one-third of the open mat is occupied by a low shrub heath in which *Cassandra calyculata* is dominant. *Andromeda glaucophylla, Kalmia polifolia,* and *Vaccinium myrtilloides* are other shrubs occurring in this zone. *Eriophorum virginicum* and *Sarracenia purpurea* are typical herbs. *Sphagnum capillaceum, S. magellanicum,* and *S. recurvum* form a continuous carpet beneath the shrubs, and at places *Polytrichum juniperinum* var. *gracilius* and *Sphagnum fuscum* have built up hummocks. *Larix laricina* and *Pinus Strobus* seedlings are present throughout the low shrub zone. An island of *Larix laricina* trees 4 to 6 in in diameter occurs near the middle of the mat and extends eastward and southward. Large *Pinus Strobus* trees are present on humified peat along the west and northwest sides near the edge of the basin. *Picea mariana* does not occur at this bog.

Much of the upland around the basin was formerly under cultivation, although conifer stands planted during reforestation projects and secondary forests developing on abandoned fields currently occupy much of the area. The woodlot to the east and southeast of the bog is the least modified of any nearby forest remnant. On muck in the lower areas, *Acer rubrum, Betula alleghaniensis, Carpinus caroliniana, Prunus serotina,* and *Tsuga canadensis* are the principal trees. Typical herbs in this area include *Clintonia borealis, Coptis groenlandica, Oxalis montana, Medeola virginiana,* and *Trillium undulatum.* Upslope on better drained soil, *Acer saccharum* and *Fagus grandifolia* are abundant, and they occur with *Fraxinus americana, Tilia americana,* and *Tsuga canadensis.* Plantations of *Pinus resinosa, P. Strobus,* and *Larix decidua,* interspersed with untilled fields, occur south, east, and north of the bog. To the west and northwest, contiguous with the bog, is a narrow zone of open swamp forest in which *Acer rubrum* and *Ulmus americana* are the dominant trees. *Populus grandidentata* and *Crataegus* sp. are common at disturbed sites and abandoned fields around the bog.

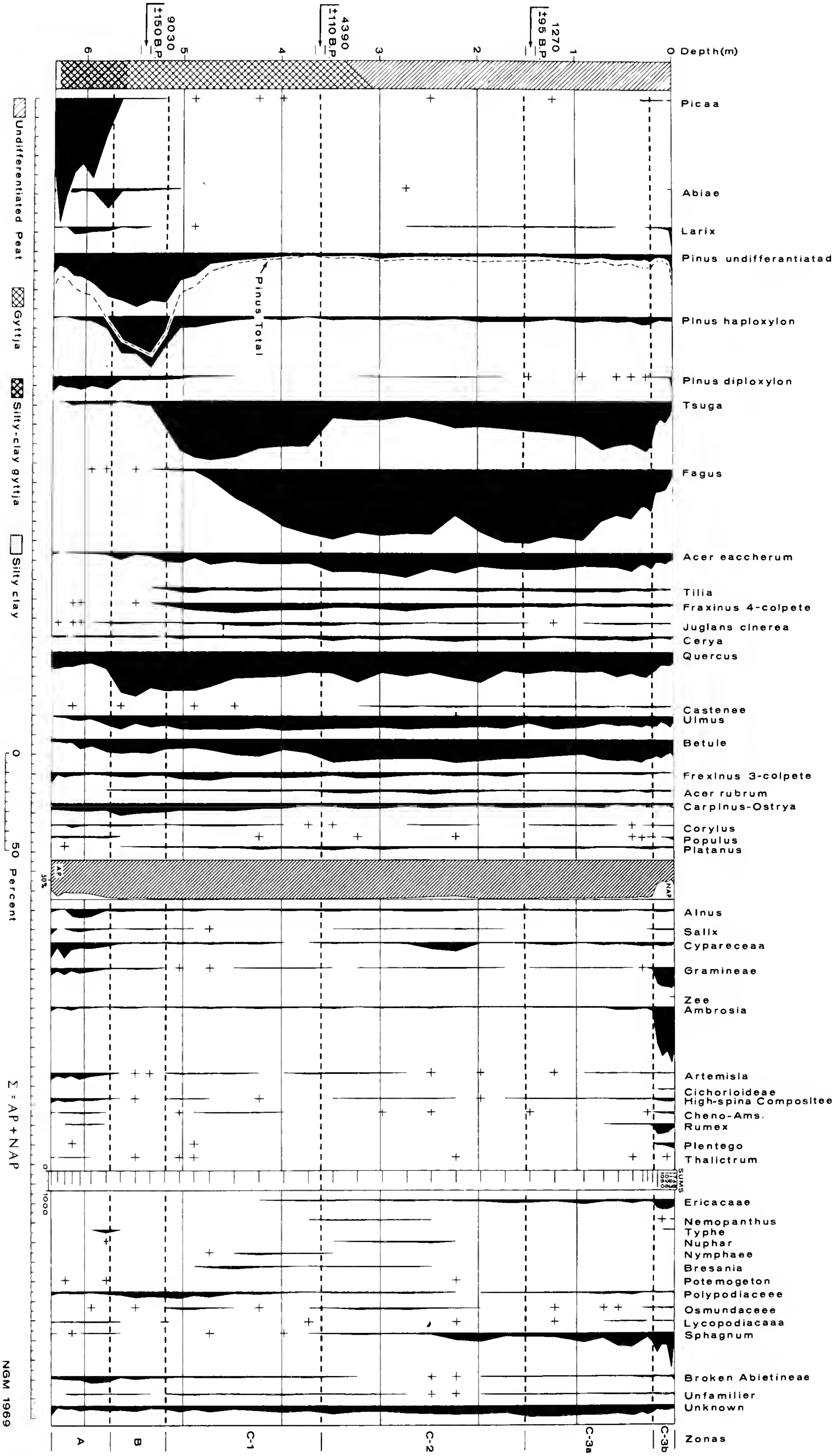
Sediment Stratigraphy

The bog was sampled on August 24, 1967, near the center of the basin. The Hiller sampler was used from the surface downward to 6 m, but, because of the compactness of the sediments, it was necessary to substitute the Davis head attached to the Livingstone extension rods to sample beyond this depth. The stratigraphy at the sampling point is:

Diagram 1

Protection Bog: Relative Pollen Frequency

0.00–0.10 m	:	peat, with sphagnum leaves, humified, dark brown;
0.10–0.90 m	:	peat, undifferentiated but with sphagnum leaves, reddish brown;
0.90–3.25 m	:	peat, undifferentiated but with sedge leaf fragments and other plant debris, coarse near the top but



PROTECTION BOG: RELATIVE POLLEN FREQUENCY

gradually becoming finer downward, reddish;

3.25–6.30 m : gyttja, soft, somewhat gelatinous, brown at top, gradually becoming stiffer and rubbery downward, with *Najas* seeds from 4.75 to 5.40 m, silt and clay admixture beginning at 5.60 m, mostly brown or reddish brown;

6.30–6.33 m : silty-clay, with some medium sand at bottom; bluish-gray. The sediments could not be penetrated farther with equipment used.

Houghton Bog

Located 12 mi southwest of Protection Bog, Houghton Bog occupies an ice-block depression in a pitted outwash plain which extends southward from the Valley Heads moraine past the village of Springville to Cattaraugus Creek. Houghton Bog is one of the larger of the many basins which dot this plain. Most of the depressions have filled with sediment, but several open lakes are also present. Of these, Dead Mans Lake is most prominent. The outwash fan forms a minor divide, separating drainage in a general northward direction to Eighteen Mile Creek and the West Branch of Cazenovia Creek from drainage southward to Cattaraugus Creek.

Houghton Bog is situated in the Town of Concord, 2.3 mi north of Springville between US 219 and Sharp Street at 42° 32′ 30″ N. lat. and 78° 40′ 13″ W. long. and is shown as an area of wooded marsh on the Springville 7½′ quadrangle. The basin occurs in a forest remnant about 45 acres in area, which is completely surrounded by tilled and fallow fields. Little of the original forest remains within a 3 mi radius of the bog. The basin, as measured on an aerial photograph, covers about 18 acres. The shoreline occurs between the 1400 and

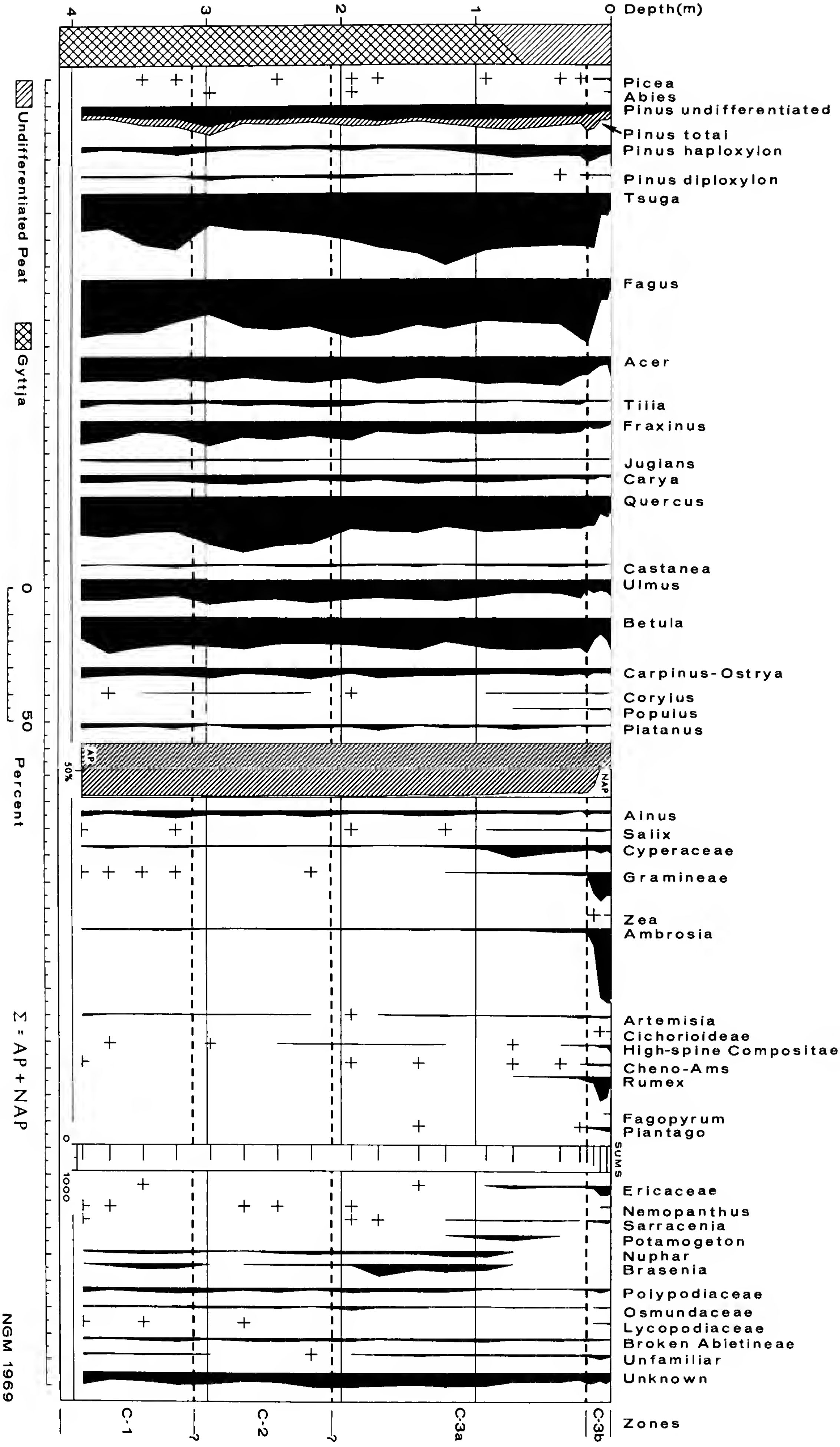
Figure 5

1410 ft contour lines. Except for about 5 acres occupied by an open mat (figure 5), the depression is now entirely forested. The bog is owned by the Nature Sanctuary Society of Western New York, Inc., which attempts to maintain it in an unmodified condition.

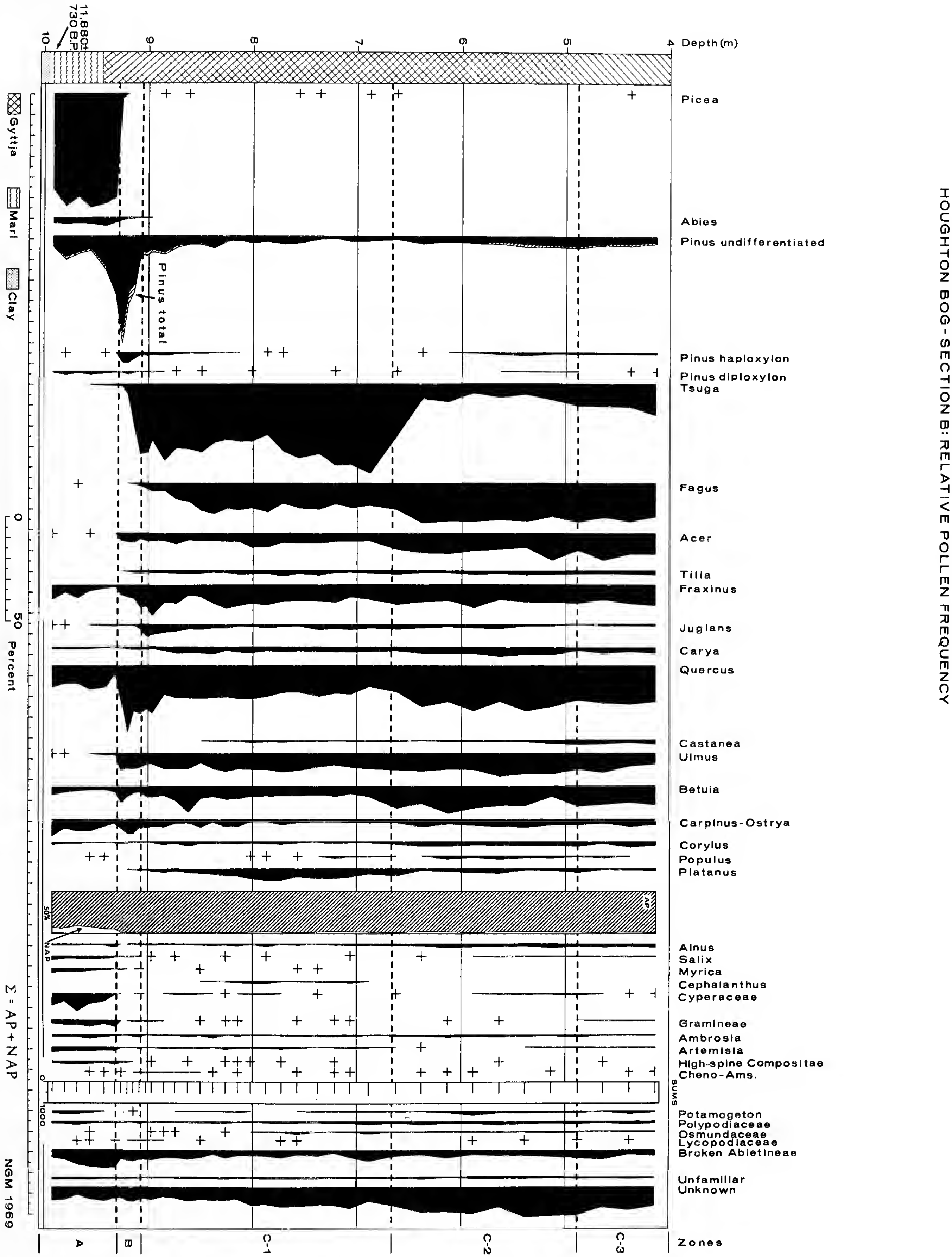
The long axis of the basin has a north-south orientation. Beyond the main depression, two shallow bays extend to the north and south (Brosius, 1953). These must have rapidly filled with sediment for the upper layer is strongly humified and now supports a swamp forest. The 5 acre bog mat extends entirely across the surface in a northwest-southeast direction. The mat is thinnest near the southeast end where the weight of a man is sufficient to cause water to seep upward. No permanent outlet or inlet is present, although a low area which apparently is the route for excess spring runoff extends southward to join a tributary of Spring Brook. The slopes immediately above the basin are gentle. The surface of the outwash plain is rolling and uneven and in general no more than 20–30 ft above the mat surface. Nearby hills rise about 300 ft above the surface of the plain.

The bog is surrounded by a strip of forest of variable width. On the slope above the mat, the main tree species are *Acer saccharum, Betula alleghaniensis, Fagus grandifolia, Prunus serotina, Tsuga canadensis,* and *Ulmus americana.* Adjacent to the north and northeast bog margin occurs a somewhat larger woodlot. This stand was heavily logged in the past and is now occupied by trees of small diameter, mostly *Acer saccharum* and *Fagus grandifolia.* A few *Prunus serotina* trees are also present, and *Tsuga canadensis* seedlings were noted. On the wetter, organic-rich soil between the edge of the basin and the open mat, a swamp forest of *Acer rubrum, A. saccharinum, Betula alleghaniensis, Pinus Strobus, Prunus serotina, Tsuga canadensis,* and *Ulmus americana* occurs. At places in the swamp forest, *Taxus canadensis* forms a dense cover. *Pinus Strobus* is particularly abundant along the south and west margins of the bog mat.

A narrow high shrub zone of *Nemopanthus mucronata, Pyrus melanocarpa,* and *Viburnum cassinoides* occurs between the swamp forest and the open mat. *Cassandra calyculata* is the dominant shrub throughout most of the open mat, but *Kalmia polifolia, Vaccinium myrtilloides,* and *V. Oxycoccos* are also present. *Carex canescens, C. pauciflora, C. trisperma, Rhynchospora alba, Sarracenia purpurea,* and various bog orchids are restricted to certain parts of the mat. The main *Sphagnum* species include *S. capillaceum* var. *tenellum, S. fuscum, S. magellanicum,* and *S. teres; S. cuspidatum*



HOUGHTON BOG-SECTION A: RELATIVE POLLEN FREQUENCY



HOUGHTON BOG - SECTION B: RELATIVE POLLEN FREQUENCY
Depth (m)
10
9
8
7
6
5
4
11,880±730 B.P.
Picea
Abies
Pinus undifferentiated
Pinus total
Pinus haploxylon
Pinus diploxylon
Tsuga
Fagus
Acer
Tilia
Fraxinus
Juglans
Carya
Quercus
Castanea
Ulmus
Betula
Carpinus-Ostrya
Corylus
Populus
Platanus
AP
50%
NAP
Alnus
Salix
Myrica
Cephalanthus
Cyperaceae
Gramineae
Ambrosia
Artemisia
High-spine Compositae
Cheno-Ams.
SUMS
0
1000
Potamogeton
Polypodiaceae
Osmundaceae
Lycopodiaceae
Broken Abietineae
Unfamiliar
Unknown
Zones
A
B
C-1
C-2
C-3
Gyttja
Marl
Clay
0
50
Percent
Σ = AP + NAP
NGM 1969

occurs in the wetter areas near the southeast end. *Pinus Strobus* seedlings are abundant on the grounded mat; *Larix laricina* is restricted to the southeast and northeast corners of the mat. *Picea mariana* does not occur at Houghton Bog.

Sediment Stratigraphy

Because of a water pocket beneath the mat, two series of samples were collected at Houghton Bog. Section A was taken on October 17, 1966, with the Hiller sampler near a small stand of tamarack located one-half the distance toward the center of the basin, 56 m S. 10° E. of the sampling point for section B. The stratigraphy of section A is:

Diagram 2

Houghton Bog — Section A: Relative Pollen Frequency

0.00–0.10 m :	peat, humified, dark brown;
0.10–0.60 m :	peat, undifferentiated but with sphagnum leaves, light reddish brown;
0.60–0.85 m :	peat, undifferentiated but with sedge leaf fragments, somewhat coarse grading downward into finer texture, gray to dark gray;
0.85–4.00 m :	gyttja, soft, with some sedge leaf debris near top, becoming stiffer downward, gray.

Section B was collected on September 1, 1966, somewhat east of the center of the open mat using a Hiller sampler between 4.00 and 8.00 m and a Livingstone piston corer with a 2 in tube beyond 8.00 m. The stratigraphy at this point is:

Diagram 3

Houghton Bog — Section B: Relative Pollen Frequency

Diagram 4

Houghton Bog—Section B: Absolute Pollen Frequency

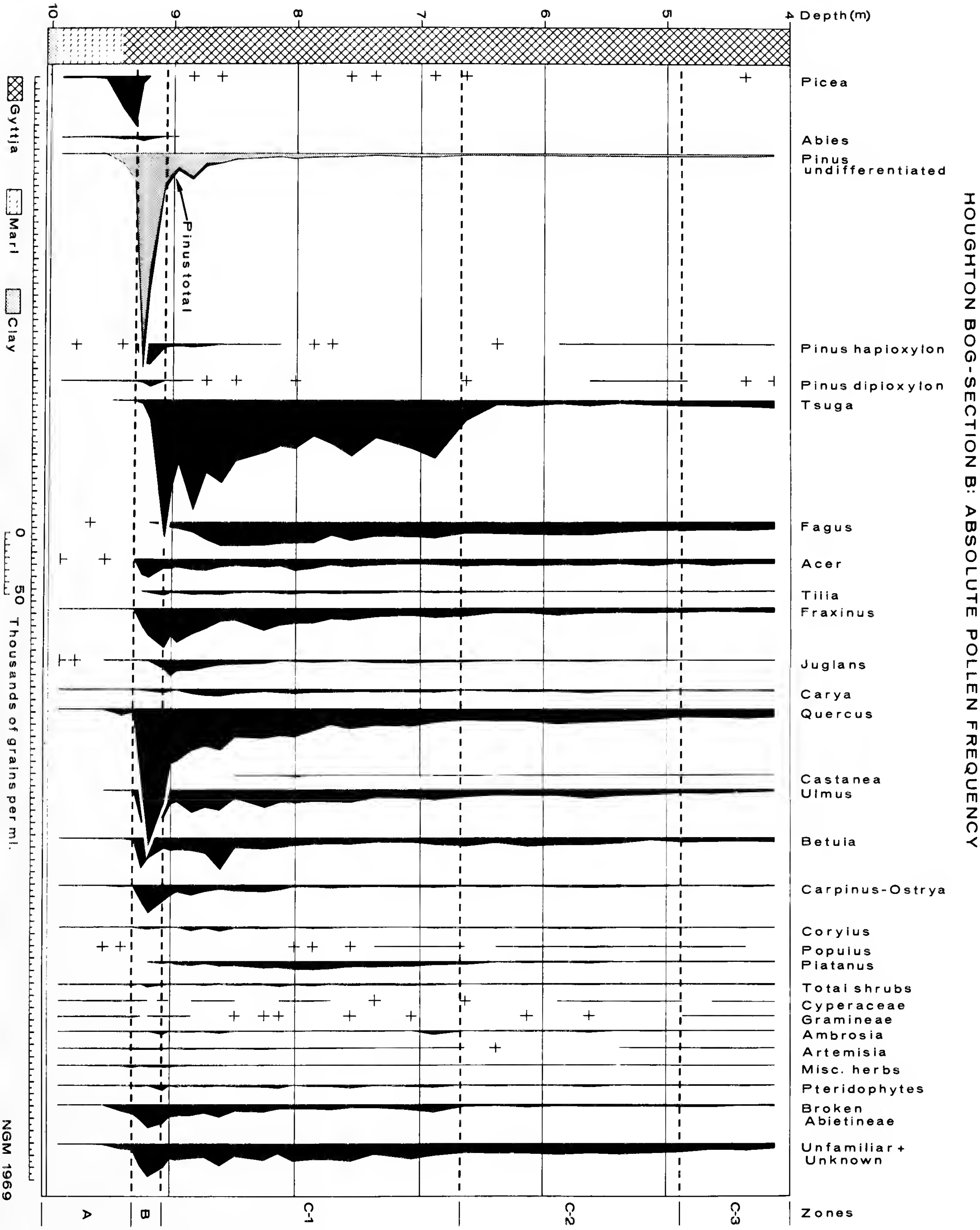
0.00–0.75 m :	peat, watery, fibrous, with sphagnum leaves, no samples taken;
0.75–4.00 m :	finely comminuted plant debris in water, few seeds present near bottom, no samples taken;
4.00–9.43 m :	gyttja, soft and gelatinous at top with small amount of plant debris, gradually becoming stiffer and more rubbery downward, brownish throughout;
9.43–9.95 m :	marl, with dark brown and reddish laminae; Mollusca and charophyte oogonia abundant, strongly calcareous, whitish gray;
9.95–10.04 m :	clayey silt, dense with gravel near bottom, carbonized wood fragments present sporadically, mostly dark gray but somewhat brownish, sharp contact with marl above. Further penetration impossible.

Pollen Stratigraphy

In the following discussion, pollen diagrams have been divided into zones using the letter designations that Deevey (1939) first applied to his New England pollen profiles. These have found wide usage in the Northeast. Zone C, the uppermost, is characterized by pollen of hardwoods and hemlock and can generally be subdivided into three main parts. Below this in order are zone B which is dominated by pine pollen and zone A in which abundant spruce pollen is found. Zone T (Leopold, 1956b) is an interval beneath the A zone in which NAP percentages are high.

I am aware of the recent trend toward describing pollen assemblage zones from bog and lake sediments in accord with the Code of Stratigraphic Nomenclature (see Cushing, 1967) rather than extending the use of letter zone designations developed in one region to distant geographical areas. But I feel, as does Livingstone (1968), that zones are " to be regarded as temporary divisions of convenience, to be used as reference points in discussions of the underlying trends in the pollen curves . . . [and that they] . . . should not be enshrined under the protection of a code involving strict rules of description and priority " (p. 95). There are chronological reasons, and perhaps climatic ones as well, for extending Deevey's zones to western New York. It should be understood, however, that floristically and vegetationally, the zones are not the same in New England and western New York nor, for that matter, in most other places where they are used. This is clearly brought out by Deevey (1957) in a summary table in which he compares pollen sequences from northern Maine, southern Connecticut, and Michigan by subdividing them into A, B, and C zones.

Because of the close similarity between the pollen diagrams for Protection (diagram 1) and Houghton bogs (diagrams 2, 3, and 4), they will be discussed together. Minor pollen types not included in the diagrams are listed in appendixes H, I, and J.


HOUGHTON BOG-SECTION B: ABSOLUTE POLLEN FREQUENCY
Depth (m)
10
9
8
7
6
5
4
Picea
Abies
Pinus undifferentiated
Pinus total
Pinus haploxylon
Pinus diploxylon
Tsuga
Fagus
Acer
Tilia
Fraxinus
Juglans
Carya
Quercus
Castanea
Ulmus
Betula
Carpinus-Ostrya
Corylus
Populus
Platanus
Total shrubs
Cyperaceae
Gramineae
Ambrosia
Artemisia
Misc. herbs
Pteridophytes
Broken Abietineae
Unfamiliar + Unknown
Zones
A
B
C-1
C-2
C-3
Gyttja
Marl
Clay
0
50
Thousands of grains per ml.
NGM 1969

Zone A. In the lowermost spectra at both bogs, 40 to 50 percent of the sum is comprised of *Picea* pollen. It is about five times more abundant than pollen of any other type. Although both records may be truncated at the bottom, there is no clear indication of a T zone beneath zone A at either site. At Protection Bog, however, the abrupt decline in the spruce curve which, below the maximum at 6.265 m, is caused by a 25 percent NAP high may, in part, record the transition from herb- to spruce-dominated vegetation. The number of terrestrial pollen grains and spores rises rapidly from about 18,000 to 140,000 grains/ml of wet sediment between 6.325 and 6.195 m. Assuming a constant rate of sedimentation across this interval, the change parallels that reported for Rogers Lake, Connecticut during the T to A zone transition (Davis, 1967b).

At Houghton Bog a similar change occurs, but it is not as readily interpreted (diagram 4). The deepest sediment sampled at this location was a dark gray, silty clay, apparently barren of pollen. Upward, passing abruptly into marl, the number of grains per unit volume is at first very low, 2000 to 3000 grains/ml (figure 6), but rises to 60,000 grains/ml in the first gyttja sample immediately above. Because of the change in sediment stratigraphy, it is unlikely that the rate of sedimentation was constant from the clay upward through the marl to the base of the gyttja. It seems probable that the marl was deposited rapidly, resulting in a lower number of pollen and spores per unit volume. Unfortunately, close interval radiocarbon dating is the only method at present which can be used to determine accurately the sedimentation rate, and age determinations are not available for Houghton Bog. However, at Rogers Lake (Davis & Deevey, 1964; Davis, 1967b), Seth's Pond, Massachusetts, and Silver Lake, Ohio (Ogden, 1967a), fairly uniform rates have been demonstrated. These involve about a twofold to threefold increase from the late-glacial time through nearly all of the postglacial except the most recent.

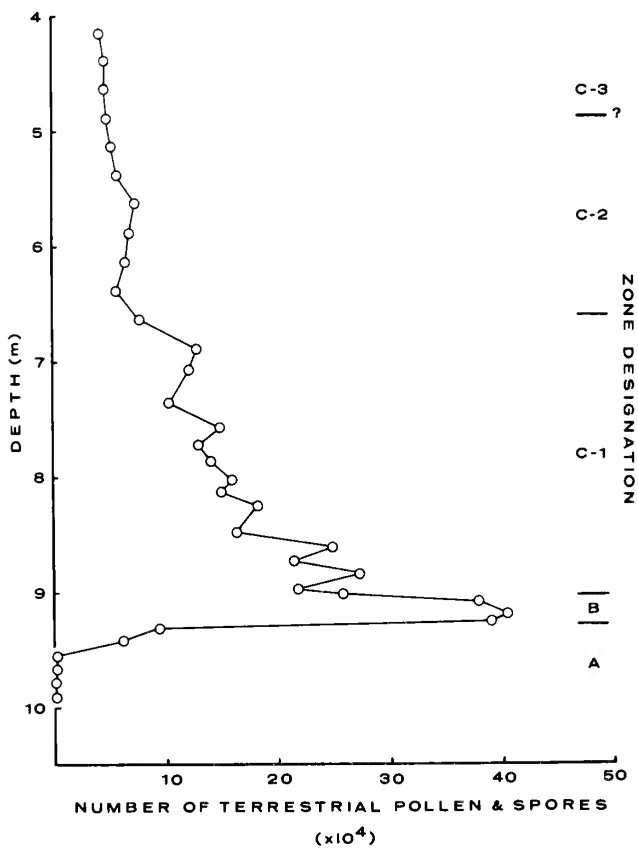


Figure 6

At Protection Bog, possible subdivision of the A zone into a *Picea-Abies* subzone is suggested by the prominent peak in the *Abies* curve near the top of the zone. The greatest percentage of *Abies* pollen at Houghton Bog also occurs in the upper part of the A zone. *Larix,* although not encountered in zone A sediments at Houghton Bog, accounts for about 5 percent of the sum in the middle portion of the A zone at Protection Bog, decreases upward, and finally drops out of the counts in zone B. *Pinus* pollen regularly comprises 10 to 15 percent of the total in the lower levels of both bogs, but, upward, its percentage gradually increases until the maximum is reached in zone B.

Three different categories of pine pollen were counted. The basic separation was between grains which could be identified as belonging to the softwood pines, *Pinus* subg. Strobus, which in northeastern North America includes only *Pinus Strobus* (see Little & Critchfield, 1969) and the hardwood pines, *P.* subg. Pinus, which in this region includes *P. Banksiana, P. resinosa,* and *P. rigida.* The germinal furrow (Ueno, 1958), located between the bladders on the distal face of the pollen grain, is verrucose in subg. Strobus (called *Pinus* haploxylon in the pollen diagrams), whereas the furrow is smooth in subg. Pinus (*Pinus* diploxylon in the diagrams). The third category, *Pinus* undifferentiated, contains grains that could not be oriented to permit observation of the furrow, those grains in which the exine between the bladders was missing, and reassembled grains (the number of which was determined by keeping track of the larger fragments and then dividing the sum of these by an appropriate figure to reduce the sum to the number of whole grains). Diagram 1 shows that pollen of subg. Pinus was most abundant in zone A. This also is illustrated in diagram 3, but less prom-

inently. The sum of the three categories is graphed as *Pinus* total.

Ulmus pollen is found in low percentages near the bottom of zone A but gradually increases to about 7 percent near the top of the zone at Protection Bog. From 1 to 2 percent *Ulmus* occurs at an equivalent stratigraphic position at Houghton Bog. About 5 percent of *Carpinus* and/or *Ostrya* pollen is present in all A zone spectra, and, at both bogs, there is a small but definite *Carpinus-Ostrya* peak near the A to B zone transition. Low precentages of *Corylus* pollen occur in all A zone spectra at both bogs. *Betula* pollen is regularly present in A zone sediments, although in fairly low percentages. At Protection Bog, *Betula* representation gradually increases upward, and, near the beginning of the B zone, a maximum is reached which persists throughout the lower part of this zone. A similar but sharper peak is present at Houghton Bog. *Populus* pollen accounts for 2 to 3 percent of zone A totals at Protection Bog.

Low percentages of tricolpate *Fraxinus* pollen occur throughout the A zone at Protection Bog. Pollen of this type, which at most sites was tabulated separately from *Fraxinus* pollen with four and five colpi, is produced mainly by *F. nigra,* judging from pollen reference slide examinations. Tetracolpate pollen is typically produced by *F. americana* and *F. pennsylvanica,* although a few 3- and 5-colpate grains are occasionally found in reference slide preparations of these species, as are some 4-colpate grains in reference slides of *F. nigra* pollen. At Houghton Bog, *Fraxinus* pollen was not differentiated in this way, but it is reasonable to assume that 4-colpate grains are as poorly represented in zone A at this site as they are at Protection Bog.

Pollen of several taxa characteristic of the Hemlock-white pine-northern hardwoods and Beech-sugar maple forest regions appear in zone A. At Protection Bog, 2 to 3 percent of *Tsuga* pollen occurs in the upper part of this zone and 1 percent or less is found in the same stratigraphic position at Houghton Bog. At one or both sites, sporadic grains of *Castanea, Fagus, Fraxinus* 4-colpate, *Juglans cinerea, Liquidambar,* and *Platanus* were also encountered. At Protection Bog, about 1 percent of *Acer saccharum* pollen is present and trace percentages of undifferentiated *Acer* grains also occur at Houghton Bog. At both sites *Carya* (ca. 1 percent) and *Quercus* pollen (ca. 10 percent) are present throughout zone A.

With the exception of the top 20 cm of the sediment column, zone A contains the highest percentages of nonarboreal pollen anywhere in the diagrams. At both bogs, pollen produced by unknown members of the Cyperaceae and Gramineae amounts to 5 to 8 percent of the total. Associated pollen types include *Ambrosia, Artemisia, Rumex, Thalictrum,* periporate grains belonging to species in the Chenopodiaceae, Amaranthaceae, or both (Cheno-Am. pollen), and other herbaceous taxa listed in appendixes H and J. Significant percentages of pollen belonging to unknown members of the Asteroideae (Compositae) are regularly present in zone A. In all diagrams, these are graphed under the heading, high-spine Compositae. From 1 to 5 percent of *Alnus* and *Salix* pollen occurs in zone A at both bogs. Low percentages of *Myrica* pollen are found throughout the A zone at Houghton Bog.

An age determination of 11,880 ± 730 B.P. (I-3290) on wood near the bottom of the marl at Houghton Bog affords a minimum date for the beginning of zone A at this site. This correlates well with a comparable date, 12,000 ± 300 B.P. (W-507; Rubin & Alexander, 1960), on wood from a marly silt in a depression on the Chaffee outwash plain near the Cheery Tavern Crossroads 10 mi to the east, although it is considerably younger than the date, 14,900 ± 450 B.P. (I-4216), recently reported by Calkin (1970) from the same site. Mollusks found in the marl at the Cheery Tavern locality indicate the sediment accumulated near the margin of a heavily vegetated pond. Pollen analysis and the fossil snails suggest a climate somewhat cooler than the present prevailed at the time of deposition (Daily, 1961). Remains of a mastodon were also uncovered at this site.

The Mollusca which occurred in the marl at Houghton Bog were not identified, but charophyte oospores, removed from the residue after HCl treatment, and part of the original core were sent to Fay Kenoyer Daily for study. The collection contained only *Chara sejuncta* A. Br. (Daily, 1968, and letter, April 11, 1968), a species that often grows in ponds with mud bottoms at the present time (Daily, 1961). Wood (1965) reports that *C. sejuncta* ranges from Massachusetts to the Great Lakes southward to the West Indies, Brazil, and Uruguay, and its distribution in New York State is given by Wood and Muenscher (1956).

Zone B. Pine pollen dominates zone B at both bogs, although substantial percentages of *Quercus* pollen are also present. The boundary separating zones A and B was drawn where *Quercus* pollen begins to increase. This also is at about the middle of the *Picea* decline which marks the demise of spruce in the area. Pine pollen accounts for about 50 percent of the total in zone B; oak pollen for an additional 20 percent. High

percentages of *Pinus* subg. Strobus pollen indicate that *P. Strobus* was the dominant pine surrounding the sites when B zone sediments accumulated. At Protection Bog, a *P. Strobus* cone was found at 5.75 m in stiff gyttja collected with a 2-in diameter Livingstone corer that was being used to obtain material for radiocarbon assay. The presence of white pine immediately adjacent to the basin during early zone B time is clearly established.

Small but significant percentages of *Ulmus* and *Carpinus-Ostrya* pollen occur in zone B and a slight increase in the amount of birch pollen across the A to B zone transition is present. Only 2 percent of the total pollen in the B zone is contributed by nonarboreal species. In both diagrams this amount continues to occur upward to the presettlement to postsettlement boundary.

Diagram 4, in which the number of grains per ml of wet sediment is plotted, shows that the greatest numbers of pollen grains in the B zone were contributed by *Pinus* and *Quercus*. *Pinus* reaches a maximum of 176,000 grains/ml at 9.25 m. At Protection Bog, the B zone *Pinus* peak has been dated at 9030 ± 150 B.P. (I-3551).

Zone C-1. The boundary between zones B and C-1 is drawn at the middle of the *Tsuga* increase. Pine pollen at this point still accounts for about 30 percent of the total, but it subsequently decreases to 7 percent in the lower third of zone C-1 and to about 3 percent at the end. *Abies* pollen disappears in the beginning of zone C-1. The percentage of *Quercus* remains high and amounts to nearly 20 percent of the total at Protection Bog. Its decline is gradual at this site and, with a slight lag, parallels that of *Pinus*, although at the end of the C-1 zone, *Quercus* still accounts for 10 percent of the total. A similar pattern in the curve for this species occurs at Houghton Bog. The lower third of C-1 is dominated by pollen of *Tsuga*, *Quercus*, and *Pinus*. Upward, percentages of *Quercus* and *Pinus* pollen decrease and are replaced in part by *Fagus* pollen, which at the end of zone C-1 accounts for 35 percent of the total at Protection Bog and about 10 at Houghton Bog.

At the beginning of zone C-1 at Houghton Bog are maxima in the curves for *Fraxinus* and *Juglans*. *Fraxinus* is strongly represented through much of the zone, and, at Protection Bog, the highest C zone percentages of *Fraxinus* 4-colpate occur in the C-1. At both bogs *Betula* increases somewhat over lower levels and it reaches a peak in the lower half of the zone. Represented in all C-1 spectra in amounts ranging from 5 to 10 percent are *Acer*, *Ulmus*, *Carpinus-Ostrya*, and *Carya*. Both *Acer rubrum* and *A. saccharum* are present at Protection Bog in this zone. Smaller percentages of *Tilia* and *Corylus* occur throughout. At Protection Bog there is a *Tilia* maximum of modest size at the beginning of zone C-1.

Castanea first appears in the lower half of zone C-1 at Houghton Bog, and, although sporadic grains occur in the same zone and at lower levels at Protection Bog, *Castanea* was not regularly encountered in the counts until just above zone C-1 at this site. The highest percentages of *Platanus* pollen found occur near the middle of this zone at Houghton Bog and a similar but smaller peak occurs at about the same stratigraphic position at Protection Bog. At both bogs fairly high percentages persist into the lower part of zone C-2.

As shown in diagram 4, *Tsuga* contributed the greatest number of pollen grains of any one type per ml of sediment in zone C-1 at Houghton Bog. Upward, from zone B to zone C-1, *Tsuga* replaces *Pinus* and *Quercus* as the major component of the pollen rain.

Zone C-2. The middle of the prominent *Tsuga* decline was chosen to mark the C-1/C-2 boundary, and, at Protection Bog, this point has been dated at 4390 ± 110 B.P. (I-3550). Associated with the decreasing *Tsuga* percentages at both bogs are increases in the *Acer*, *Betula*, *Carya*, *Fagus*, and *Quercus* curves. At Protection Bog, where species of *Acer* were identified, percentages of *A. saccharum* pollen are greater and increase more than those of *A. rubrum*. The number of *Tsuga* grains per ml decreases from 30,000 to 5,000 across the C-1/C-2 transition. Small increases in the number of grains per unit volume for *Fagus*, *Acer*, *Quercus*, and *Betula* are evident.

At Protection Bog, there is a small decrease in the percentage of *Fagus* pollen at about the middle of zone C-2. This probably does not reflect a decrease of *Fagus* in the surrounding forest as the decrease is mainly compensated for by an increase in Cyperaceae pollen, which is most likely of local origin. Other than the two spectra at Protection Bog in which Cyperaceae pollen accounts for about 7 percent of the total, NAP percentages average less than 3 percent of sums in zone C-2.

Zone C-3. It is difficult to place the C-2/C-3 boundary, but at both sites it was drawn after the decline of *Quercus* which was taken to mark the end of zone C-2. *Tsuga* percentages increase across this interval. At Protection Bog, these changes are dated at 1270 ± 95 B.P. (I-3549).

It cannot be conclusively determined whether sediments of zone C-3 are represented in diagram 3 for Houghton Bog because of the obvious absence of the

upper spectra. Diagram 2 was prepared to overcome this deficiency. The exact relationship between diagrams 2 and 3 can perhaps be determined only by radiocarbon dating, but examination of the pollen curves in relation to the complete diagram for Protection Bog indicates that zones C-3, C-2, and probably part of C-1 are present in diagram 2. In the absence of dates, however, the boundaries have been drawn to indicate their questionable positions. The best markers in diagram 2 are the low in the *Tsuga* curve and the corresponding highs in the *Carya, Fagus,* and *Quercus* curves. The percentages are about the same magnitude at the edge and at the center of the basin.

Zone C-3 has been divided into two subzones. In subzone C-3a, the lowest, *Tsuga* increases to 25 percent and *Fagus* correspondingly decreases at both sites. At Protection Bog, *Quercus, Betula, Carya,* and *Acer saccharum,* which decrease slightly at the C-2/C-3 transition, increase somewhat toward the end of the C-3a. These changes are not evident at Houghton Bog.

The C-3a/C-3b boundary records the influx of settlers to the area and associated forest clearance. The change is quite abrupt and (above the boundary) about 50 percent of the total pollen is contributed by nonarboreal species, mainly those associated with agriculture. Since the percentage base includes both AP and NAP, decreases in tree taxa percentages are directly related to the large numbers of NAP.

At both sites *Ambrosia* accounts for about 25 percent of the total. Other important herbaceous taxa include Gramineae (incl. Cerealia), *Rumex,* and *Plantago.* The latter is perhaps the best zone marker since it appears abruptly at the presettlement to postsettlement boundary, although occasional grains are found in zone C below this level. Cheno-Am. pollen also occurs in the C-3b and the small increases in *Artemisia* and high-spine Compositae may be attributed to introduced, weedy species. *Zea* occurs in this zone at both bogs, and *Fagopyrum* was found in the surface spectrum at Houghton Bog. Clay- and silt-sized mineral particles, presumably blown into the basin, were abundant in subzone C-3b at both bogs.

Populus and *Picea* pollen reappear in upper C-3 spectra. Increases in percentages of *Acer, Betula, Larix,* and *Pinus* occur at one or both sites between 2.5 and 7.5 cm levels and the surface. In spite of the absence of mature trees in nearby forests, a few *Castanea* grains were found in the surface samples at both bogs.

SITES ASSOCIATED WITH PRE-VALLEY HEADS MORAINES

Allenberg Bog

Situated in Cattaraugus County in the Town of Napoli a few miles north of the Wisconsin drift limit, this bog occupies a deep, northeast-southwest trending basin about 10 acres in extent at the outer edge of an area mapped as Kent (Binghamton) moraine by MacClintock and Apfel (1944). It is approximately 30 mi southwest of Houghton and Protection bogs and is shown on the southeastern quarter of the New Albion $7\frac{1}{2}'$ quadrangle at 42° 15′ 4″ N. lat. and 78° 52′ 57″ W. long. as a small lake with a marsh on the southwest side, 2.7 mi south of New Albion and 1.2 mi north of the Pigeon Valley Cemetery. A lake which occurs near the northeast end of the basin is about 40 m in diameter.

Less than one-half mile north of Allenberg Bog is Waterman Swamp, a roughly triangular tract of swamp and bog forest about 300 acres in extent. The swamp probably began as a lake ponded between drift deposits to the south and north. The basin occupied by Allenberg Bog does not seem to have been connected originally to the lake and at present is separated from the swamp by a hill and other intervening high ground. Since both occur at 1620 ft A.T., however, a possible connection may have been present around the south and east edge of the upland. A small bog lake, Black Pond, is located at the west end of the swamp.

The bog occurs in a valley above which hills to the east and west rise 250 to 300 ft. The valley floor in the vicinity of Allenberg Bog is slightly higher in elevation than the area to the south permitting drainage in this direction through Cold Spring Creek. Waterman Swamp is the headwaters of Little Valley Creek which, as an outlet, functions mostly in the spring carrying waters charged with humic acids to the northeast away from the swamp. The two streams eventually empty into the Allegheny River. The swamp, Allenberg Bog, and some of the surrounding land are owned by the Buffalo Audubon Society, which maintains the area as a wildlife sanctuary.

The vegetation of the region has been described by Gordon (1940) and Schick and Eaton (1963). Most of Waterman Swamp is characterized by the latter as an elm-ash-rhododendron swamp. On the several knolls which rise above the level of the swamp *Pinus Strobus* is particularly abundant, and *Betula alleghaniensis* and *Tsuga canadensis* are common associates. *Rhododendron maximum* and *Viburnum alnifolium* are typical understory shrubs in this area. Below the 1720 ft con-

Figure 7

tour, *Abies balsamea, Fraxinus nigra, Larix laricina, Picea mariana, Pyrus americana,* and *Ulmus americana* are frequent. At certain places, dense thickets of *Nemopanthus mucronata* and *Vaccinium* sp. occur. Large *Abies, Larix,* and *Picea* trees, 18, 21, and 16 in d.b.h. respectively, have been found at the southeast corner of the swamp. Black Pond is surrounded on all sides by an invading *Cassandra calyculata* heath, but an extensive sedge mat is absent. Small *Picea, Larix,* and *Pinus Strobus* trees are scattered across the heath.

At Allenberg Bog, the zonation of plant communities around the lake is fairly distinct (figure 7). Photographs in Gordon (1940) taken in the mid 1930's show a narrow low shrub zone separating the lake from the bog forest. Beavers, sometime after these pictures were taken, dammed the outlet and raised the water level high enough to kill most of the trees and many other plants then inhabiting the mat. They cut a shallow channel through the peat to the lake and constructed houses near the northeast and southeast ends of the basin. The beavers were last seen in 1951 and the disappearance of the dam has since allowed the water level to return to normal. Pollen stratigraphy seems not to have been disturbed by their activity.

Nuphar microphyllum and *Nymphaea odorata* have been reported from the edge of the open water, although currently only the former is present. A narrow quaking mat of *Carex limosa* and *Sphagnum* spp. is located along the south and southwest margin of the lake, but northward the mat becomes grounded. Here *Cassandra calyculata* and *Decodon verticillatus* are invading the open water directly. A discontinuous low shrub zone interspersed with dead trees occurs across the southwest two-thirds of the bog. *Andromeda glaucophylla, Carex* spp., *Cassandra, Decodon, Eriophorum virginicum, Ledum groenlandicum, Rubus hispidus,* and *Vaccinium macrocarpon* are the main species present. *Xyris caroliniana,* an apparent Coastal Plain disjunct, has been found near the south end of the bog mat.

Around the periphery of the basin, particularly along the north edge, *Larix laricina* and *Picea mariana* occur. Nearer the upland, they are found with *Acer rubrum, Betula alleghaniensis, Fraxinus nigra, Pinus Strobus,* and *Tsuga canadensis.* The understory shrubs in this area are *Viburnum cassinoides* and *Pyrus melanocarpa. Rhododendron maximum* is present along the west edge.

The upland vegetation has been described as a *Tsuga canadensis-Fagus grandifolia* forest with an admixture of *Acer saccharum* (Gordon, 1940). Other upland trees include *Juglans cinerea, Ulmus rubra, Fraxinus americana, Prunus serotina, Acer pensylvanicum, A. rubrum,* and *Betula alleghaniensis.* The typical forest herbs are *Dryopteris spinulosa* var. *intermedia, Lycopodium lucidulum, Mitchella repens, Medeola virginiana, Oxalis montana, Trillium undulatum, Viola incognita,* and *V. rotundifolia.* Oak forest does not occur in the nearby upland.

Cultivated fields surround the entire area and approach within 0.25 mi on the west and northeast sides of Allenberg Bog. However, about one-half of the area within a 3 mi radius of the bog is forested. A narrow strip of cutover forest occurs on the east and west sides, and a similar but more extensive forested area occurs immediately to the south. Much of Waterman Swamp has been heavily logged. Secondary forests on abandoned farmland are abundant in the area, but mature conifer plantations are rare. Southeast of Allenberg Bog, the New York State Conservation Department has flooded about 30 acres for use as a waterfowl breeding preserve.

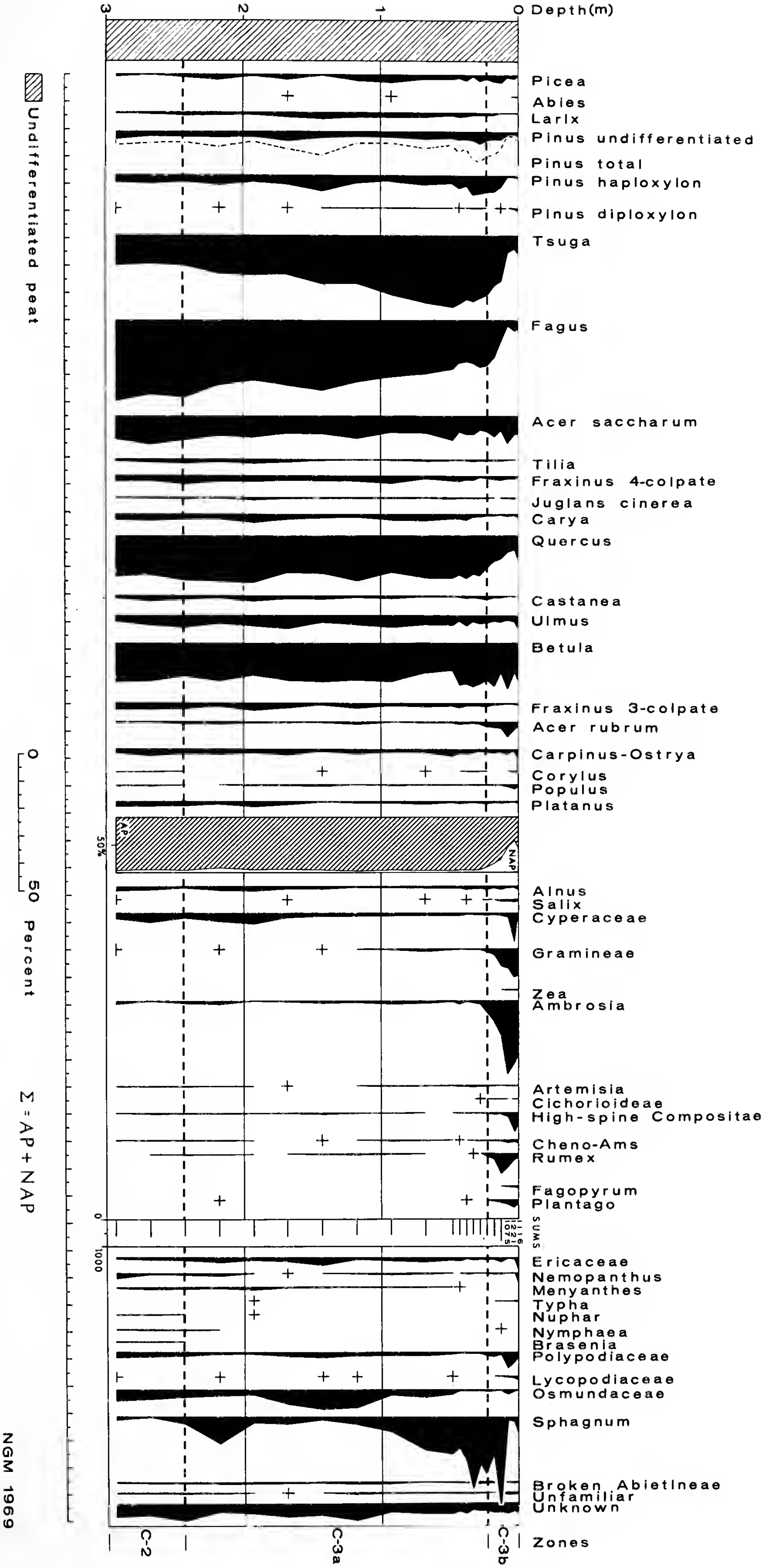
Sediment Stratigraphy

Sediments from Allenberg Bog were collected in three series. Section A was taken on October 17, 1966, with a Hiller sampler southwest of the bog lake from solid peat peripheral to the sedge mat. The stratigraphy of section A is:

Diagram 5

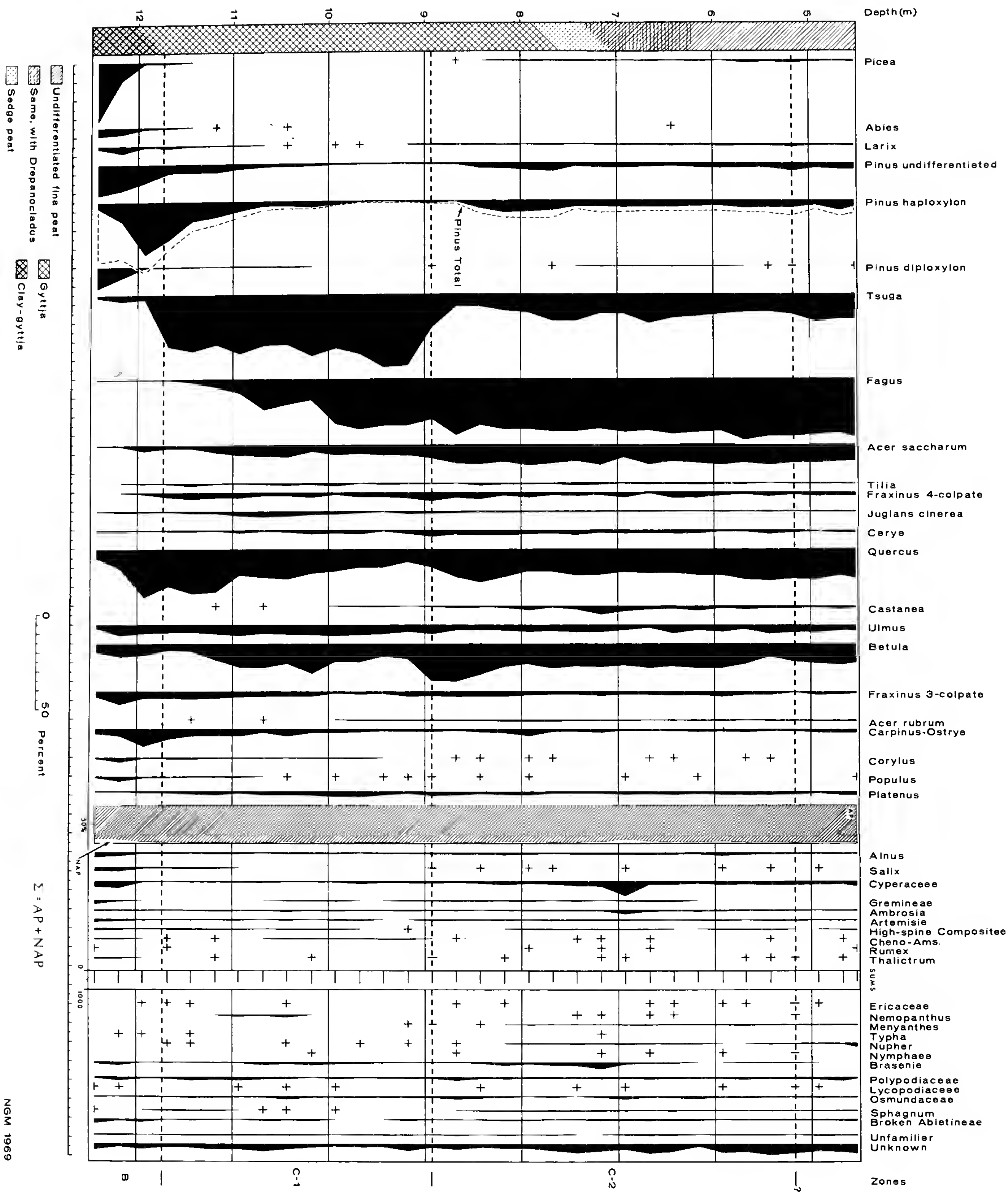
Allenberg Bog — Section A — Relative Pollen Frequency

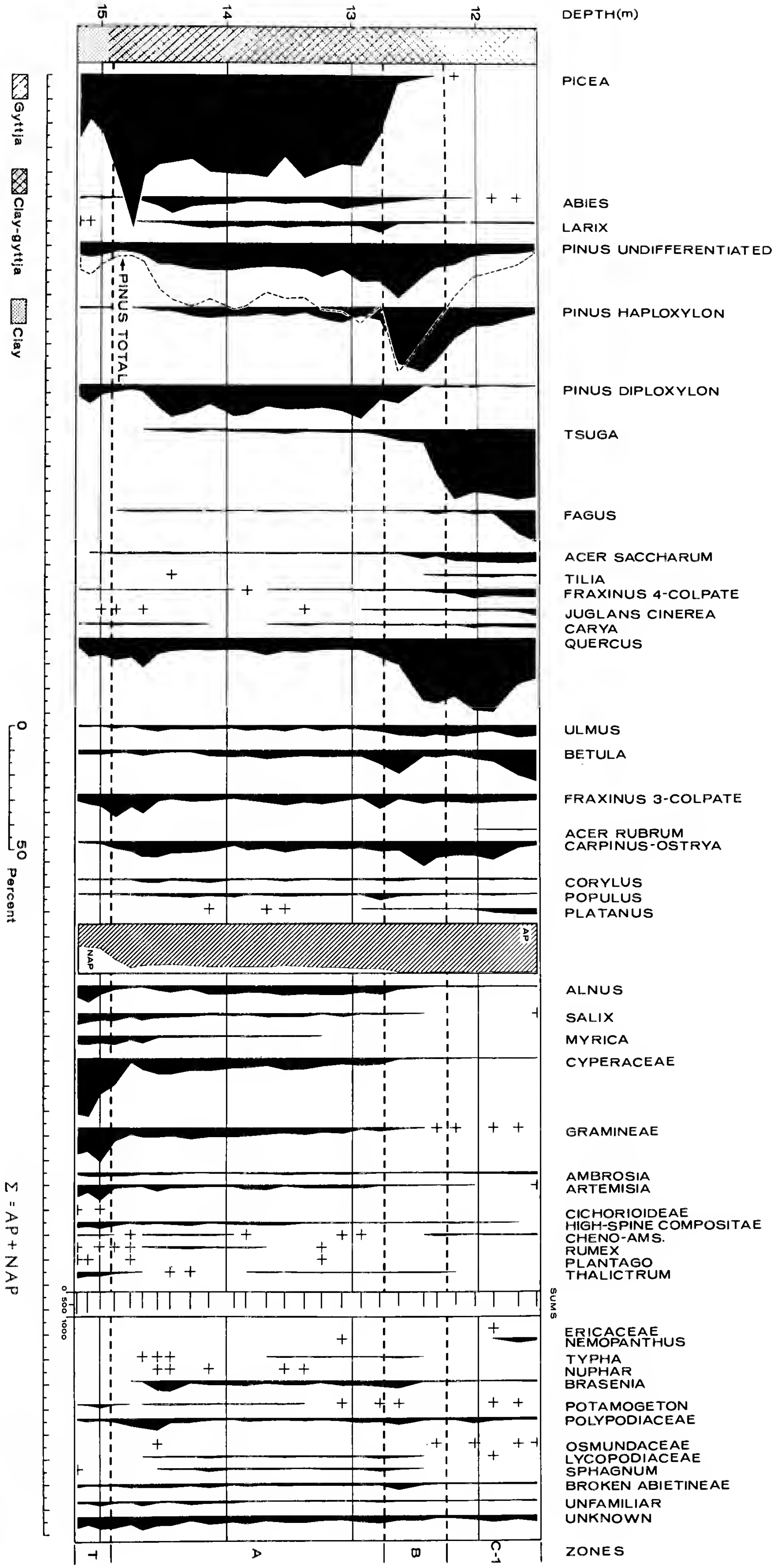
0.00–0.15 m :	peat, sphagnum leaves abundant, humified, dark brown;
0.15–3.00 m :	peat, undifferentiated, fibrous at top grading into medium to fine dissected peat downward, sphagnum leaves abundant above 1.5 m, *Drepanocladus fluitans* from 1.7 to 3.0 m, reddish brown throughout.



ALLENBERG BOG-SECTION A: RELATIVE POLLEN FREQUENCY

ALLENBERG BOG-SECTION B: RELATIVE POLLEN FREQUENCY





ALLENBERG BOG-SECTION C: RELATIVE POLLEN FREQUENCY

Section B was collected on October 15, 1966, again with the Hiller sampler, at a point 60 m N. 39° E. of section A. Sampling was discontinued at 12.5 m because insufficient extension rods were available to reach beyond this depth. The stratigraphy of section B is:

Diagram 6

Allenberg Bog — Section B: Relative Pollen Frequency

0.00–0.70 m	:	peat, fibrous, not compacted, watery, no samples taken;
0.70–4.50 m	:	water, some fine plant debris, no samples taken;
4.50–6.25 m	:	peat, undifferentiated, finely dissected, brown;
6.25–7.20 m	:	peat, undifferentiated, finely dissected but with *Drepanocladus fluitans,* brown;
7.20–7.93 m	:	peat, with abundant sedge leaf fragments, gyttja percentage increasing downward, brown;
7.93–11.90 m	:	gyttja, soft gelatinous at top, becoming stiffer downward, dark brown;
11.90–12.50 m	:	gyttja with silt and clay, dark brown.

Section C was taken through a *Cassandra* heath on April 12, 1968, 1.5 m west of the point where section B was collected. At this time more extension rods were available and the Hiller sampler was used to a depth of 14.5 m. The Davis head coupled to the Livingstone rods enabled further sampling to 15.17 m. The stratigraphy of section C is:

Diagram 7

Allenberg Bog — Section C: Relative Pollen Frequency

Diagram 8

Allenberg Bog — Section C: Absolute Pollen Frequency

11.50–12.30 m	:	gyttja, soft, dark brown;
12.30–14.90 m	:	gyttja, with increasing amounts of clays and fine sand, some plant debris present, dark brown above, becoming light brown to gray to light gray at bottom;
14.90–15.17 m	:	clay, stiff and dense, with dark brown stains, small specks of vivianite present, bluish gray. Not sampled further because of the difficulty of withdrawing the sampler from the sediments.

Pollen Stratigraphy

Zone T. The lowest sediments sampled at Allenberg Bog, including the basal clay and a portion of the clay-gyttja above, contain a pollen assemblage rich in NAP (see diagram 7 and appendix M). At 14.87 m, just above the base of the T/A zone boundary, as it was placed in the diagram, 28 percent of the sum was contributed by nonarboreal species. In the next lower spectrum, NAP increases to over 51 percent, and at 15.165 m it reaches a maximum of 55 percent.

The largest NAP contributor to the zone is the Cyperaceae, which accounts for over 20 percent of the total. Also present is about 10 percent Gramineae pollen. From 5 to 7 percent *Artemisia* pollen occurs, and *Ambrosia, Thalictrum,* and high-spine Compositae pollen are found regularly but in lower percentages in all T zone spectra. Of the less common types, pollen of the Caryophyllaceae, Chenopodiaceae-Amaranthaceae, Cichorioideae, and Labiatae; and *Plantago, Ranunculus,* and *Rumex* appear most regularly. Microspores of *Selaginella selaginoides* were found at 14.985 and 15.085 m. Pollen from the shrubs *Alnus, Myrica,* and *Salix* aggregate 15 percent of the total.

The most frequent AP type in zone T, *Picea,* accounts for nearly 20 percent of the total. About 10 percent *Pinus* pollen is present, and in general half of this is of the diploxylon type. Very low percentages of *Pinus* subg. Strobus pollen also occur. *Quercus* pollen is uniformly present in amounts which range from 5 to 8 percent. A high in the *Quercus* curve occurs near the top of the T zone and carries over to the lower A zone spectra where the A zone maximum is found. Increasing percentages of *Fraxinus* 3-colpate pollen are found from the lowest spectrum upward across the T/A zone transition where a high of 9 percent occurs. *Abies, Betula, Carpinus-Ostrya,* and *Ulmus* are weakly represented and a few grains of *Acer saccharum, Carya, Corylus, Fraxinus* 4-colpate, *Juglans cinerea, Larix,* and *Populus* occur in some or all of the spectra.

Diagram 8, which shows the number of grains per ml of wet sediment, was prepared for the same spectra graphed in diagram 7. The number of grains in the three lowest samples is relatively small and ranges from 26,000 to 40,000 per ml (figure 8). In the

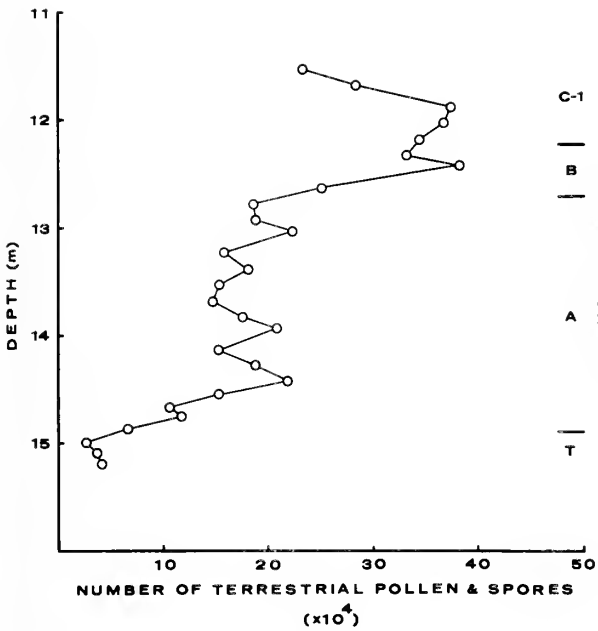


Figure 8

sediments above, the absolute number rises gradually to about 200,000 at 14.425 m near the bottom of the A zone, and it remains near this figure to the end of the zone, at which point the number of grains again increases until the maximum of about 380,000 is reached at 12.425 m. Assuming a constant rate of sedimentation, diagram 8 shows that in relation to the A zone relatively few pollen grains of any type were deposited during the accumulation of T zone sediments. The change upward into the A zone is marked not only by an increase of the percentage of spruce pollen, but also by a sixfold increase in the numbers of spruce grains being deposited. Contrary to the implication of the relative percentage diagram, larger numbers of Cyperaceae pollen occur above the T zone than within.

Zone A. Spruce pollen dominates slightly over 2 m of sediments at Allenberg Bog. It accounts for about 40 percent of the total in nearly all spectra except those near the bottom of the zone, where at one level over 60 percent was found. This peak is associated with lows in the *Pinus* total and *Pinus* diploxylon curves and high (but not the highest) percentages of *Quercus* and *Fraxinus* 3-colpate. The absolute pollen frequency diagram, however, does not show these fluctuations, although lower numbers of *Pinus* grains occur below the level of the *Picea* peak than above it.

Except near the T/A transition, *Pinus* accounts for about 20 to 25 percent of the total in all A zone spectra. Nearly half can be assigned to the diploxylon type. Haploxylon grains also occur, and, in the upper two-thirds of the zone, they account for about 5 percent of the total. Nearer the bottom, lower percentages are found.

With the exception of somewhat higher percentages in the lower part of the zone, *Quercus* averages about 7 percent of the total in all A zone spectra. Highs in *Carpinus-Ostrya, Fraxinus* 3-colpate, and Polypodiaceae curves are also present near the bottom of the zone. Two peaks in the *Abies* curve occur near the beginning (14.425 m) and end (13.075 m) of the zone. From 2 to 5 percent *Ulmus, Betula, Corylus,* and *Populus* pollen is present throughout. *Larix,* although poorly represented in lowest A zone spectra, increases to about 5 percent just below the middle of the zone and remains near this level upward to Zone B.

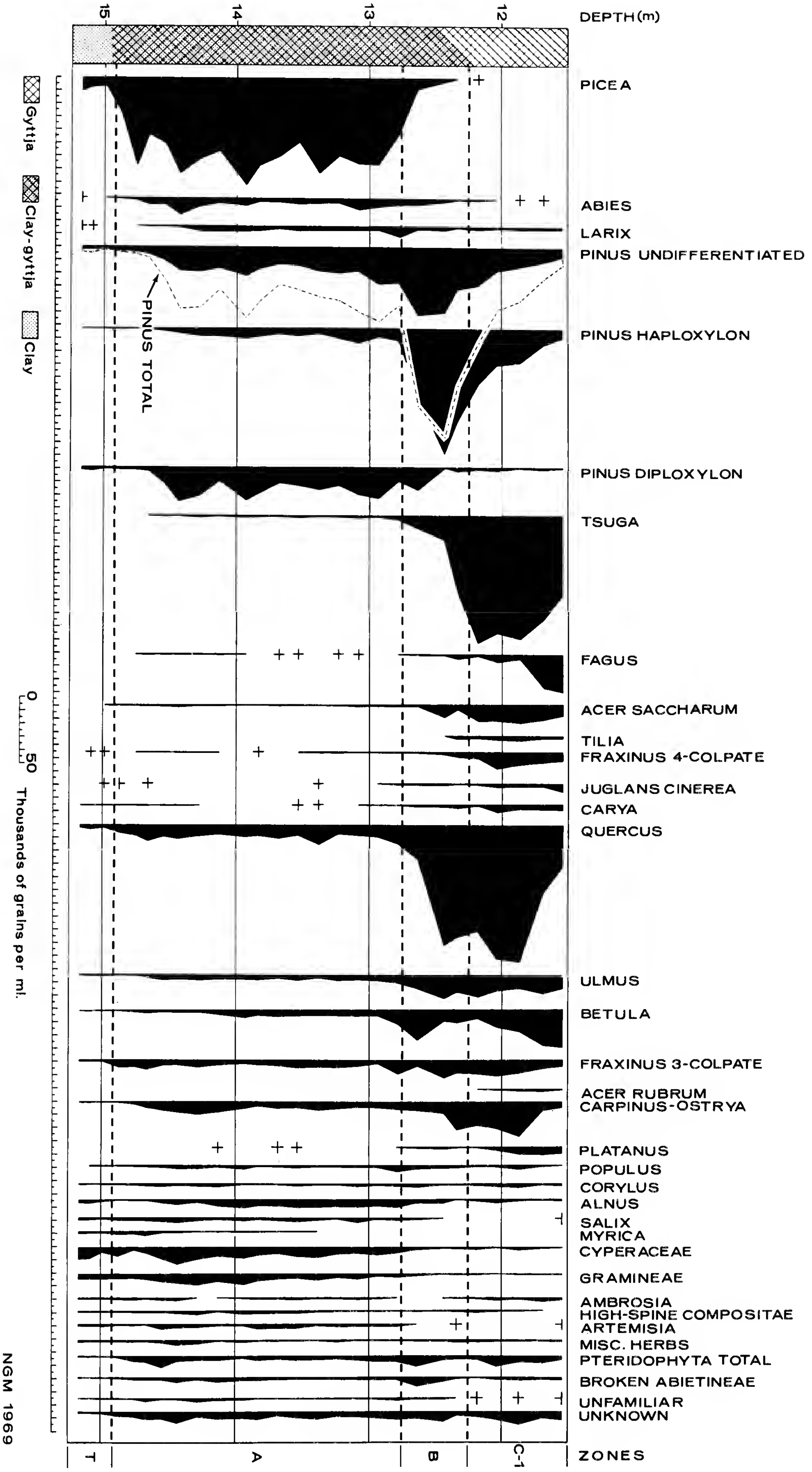
Above the T/A zone transition, total NAP percentages are about one-third of what they were in zone T. *Alnus,* Cyperaceae, and Gramineae have the highest percentages among NAP types identified. *Salix* is more weakly represented in zone A than below and it finally drops out upward in Zone B (diagram 7) or near the bottom of zone C-1 (diagram 6). High-spine Compositae, *Ambrosia,* and *Artemisia* are present in nearly all spectra. The curve for *Artemisia* has three highs at various points throughout the zone.

The relative and absolute pollen frequency diagrams agree closely across zone A.

Zone B. The change from zone A to zone B is shown in diagrams 6 and 7. In spite of the close proximity of both sample series, zone B begins 30 cm lower in diagram 7. However, percentages in both match well. Only the zone A top occurs in diagram 6.

The A/B zone transition is marked by several important changes in pollen percentages. In a span of 25 cm, *Picea* decreases from 35 to 5 percent, and it finally drops out near the end of zone B. The boundary between the two zones was drawn at the middle of the *Picea* decline which also corresponds to about the middle of the *Pinus* increase. This transition is characterized by peaks in the curves for *Betula, Fraxinus* 3-colpate, *Larix,* and *Populus. Quercus* percentages steadily increase in the lower half of zone B and reach a high of 25 percent near the end of the zone. Associated is an increase in *Carpinus-Ostrya* percentages, which remain high, but decrease somewhat in the lower part of zone C-1 over a peak reached near the end of zone B.

Total NAP percentages again decrease at the A/B zone transition and remain relatively low throughout zone B. *Alnus,* Cyperaceae, *Ambrosia, Artemisia,* high-spine Compositae, and *Thalictrum* occur most regularly.



ALLENBERG BOG-SECTION C: ABSOLUTE POLLEN FREQUENCY

In no B zone spectrum do NAP percentages rise above 2 to 3 percent of the total.

Both absolute and relative pollen frequency diagrams are similar across zone B. The high numbers of total pine pollen, which occur across a broader interval than is evident in the corresponding relative frequency diagram, help to define the zone. *Pinus* and *Quercus* are the two taxa that contributed the greatest number of grains in zone B at Allenberg Bog, as was the case at the two Valley Heads bogs discussed previously. The total number of *Pinus* grains at 12.425 m, the peak of the pine curve, is 145,000. At the same level, *Quercus* is represented by 91,000 grains.

The highs in curves for *Betula, Carpinus-Ostrya, Fraxinus* 3-colpate, and *Populus,* shown in the relative frequency diagram, also appear when the data are plotted on an absolute basis. If the sedimentation rate was constant across the A/B zone transition, these peaks occur at a time of high pollen delivery to the basin, which presumably reflects a greater abundance of plants producing these pollen types in the region neighboring the basin.

Zone C-1. Zone C-1 is completely shown in diagram 6, and, in diagram 7, the lower third is present. The B/C-1 transition is marked by rapidly increasing percentages of *Tsuga* pollen, coordinated with decreasing percentages of *Pinus* grains. However, the *Pinus* decline is not as abrupt as the increase in *Tsuga,* and there is a small interval across which the percentages of both are high. *Quercus* remains strongly represented across the transition and high percentages persist through the lower third of the zone. Near 11 m (diagram 6), *Quercus* decreases from 20 to 10 percent, while *Fagus* and *Betula* percentages increase. *Quercus* continues to decline upward through the C-1 until just below the 9 m level where only 7 percent occurs, its lowest postglacial percentage at this site. *Fagus* is weakly represented in B and lower C-1 spectra, but it begins to increase above 11.675 m after *Tsuga* becomes stabilized at near 30 percent of the sum. Near the middle of the zone, *Fagus* accounts for 13 percent of the total, but in the upper one-third of the zone, it comprises 27 percent. The curves for *Acer saccharum, Betula,* and *Juglans cinerea* show highs near the middle of the zone.

Although *Fraxinus* 4-colpate and *Tilia* first appear in zone B, the former reaches a high in the lower third of the C-1, while in the same interval *Tilia* has two minor maxima, one near the beginning and one near the end of the zone. From 3 to 5 percent *Fraxinus* 3-colpate pollen occurs regularly in the lower two-thirds of the C-1. In the rest of the zone, only about 1 percent is present. A parallel change occurs in the *Carpinus-Ostrya* curve. *Ulmus* is uniformly present in all C-1 spectra and accounts for about 7 percent of the sum. The C zone maximum for *Platanus* is reached at the end of the C-1. Percentages of *Carya* pollen, which are low at the beginning of the C-1, increase slightly upward in the zone. Except for sporadic grains in lower levels, *Castanea* occurs regularly from the upper one-third of the zone to the topmost spectrum.

Total NAP percentages vary from 1.2 to 3.6 in zone C-1. Cyperaceae and high-spine Compositae are most consistently present. Less frequently encountered pollen types are graphed in diagrams 6 and 7 or listed in appendixes L and M.

As in zone B, the relative and absolute frequency curves parallel one another (cf. diagrams 7 and 8). In that portion of the C-1 studied, the largest numbers of grains belong to *Tsuga* and *Quercus. Pinus* is also an important component of lower C-1 spectra.

Zone C-2. The boundary between this zone and C-1 can be placed readily at about the midpoint of the *Tsuga* decline, but the upper boundary of the C-2 is more difficult to locate. The gradually increasing *Tsuga* percentages which characterize the C-2/C-3 transition in the Valley Heads bogs are not evident in diagram 6, although they do occur in diagram 5. As shown in diagram 6, *Tsuga* percentages increase somewhat in the upper 0.5 m and for this reason the zone boundary made for locating it beneath the 8 m level, at which point percentages of *Quercus* and *Betula* pollen have decreased somewhat over their previous highs. However, this creates an unusually thin C-2 zone, especially when the amount of sediment above this level and a comparison between diagram 6 and the complete Protection Bog profile are taken into account. Similar reasoning suggests a part of zone C-2 may be represented in diagram 5.

At the C-1/C-2 transition, across an interval of 50 cm, *Tsuga* pollen drops from 38 to 7 percent. A small decrease in the percentage of *Ulmus* pollen is apparent across this interval also. These reductions are compensated for mainly by increases in *Acer saccharum, Betula,* and *Quercus,* and to a lesser degree by *Carya, Fagus, Fraxinus* 3- and 4-colpate, *Pinus* undifferentiated, and *Pinus* haploxylon. The *Fagus* curve shows a gradual increase from 22 percent near the end of the C-1 to 30 percent at 6 m just below the C-2/C-3 boundary. Higher percentages of *Acer saccharum, Betula,* and *Quercus* are maintained throughout the C-2 than occur in upper C-1 spectra. *Castanea* is weakly

represented across the C-1/C-2 transition, but it reaches a maximum of 4 percent at 7.175 m well into zone C-2.

Two *Tsuga* highs, each about 15 percent, occur near the middle of the C-2. These represent an increase over a low of 7 percent present near the beginning of the C-2 and a 9 percent low occurring near the end of the zone. After a sporadic presence across much of the C-1, *Larix* regularly occurs from the beginning of the C-1 to the uppermost spectrum in diagram 6. Similarly, *Picea* pollen, after an absence from all C-1 spectra except the lowest, is present in low percentages from near the beginning of the C-2 upward.

Total NAP remains low throughout the C-2. One or two percent *Alnus, Ambrosia, Artemisia,* Cyperaceae, and Gramineae pollen is most regularly present. The peak in the Cyperaceae curve just above the 7 m level may be associated with intrabasinal succession since sedge peat, which is evidence of the presence of a sedge mat at the surface, occurs just below it. The associated *Ambrosia* high is more difficult to explain, although contamination during sampling may be the cause.

Zone C-3. Zone C-3 is completely shown in diagram 5; percentages of minor pollen types are listed in appendix K. At Allenberg Bog, subzone C-3a is characterized by increasing *Tsuga* percentages which are associated with decreasing values for *Fagus.* As at the Valley Heads bogs, upper NAP rich sediments are placed in subzone C-3b; NAP percentages are minimal in subzone C-3a.

Except for minor fluctuations, percentages of most pollen types remain more or less constant across the C-3a. The percentage of *Betula* pollen increases below the C-3a/C-3b boundary and remains higher in the C-3b than in the C-3a. Together, *Picea* and *Larix* account for about 4 percent of the sum in most C-3 spectra. NAP percentages are low in subzone C-3a and average about 3 percent of the total. *Alnus, Ambrosia,* Cyperaceae, and high-spine Compositae are regularly present.

The higher percentages of Cyperaceae in the lower half of the C-3a, rather than in the upper, seem to be related to intrabasinal succession. Upward from the lowest spectrum in diagram 5, the aquatics, *Brasenia, Nuphar,* and *Nymphaea,* abruptly drop out of the counts. Above the level of their disappearance, Cyperaceae percentages increase, and above this, increases occur in the curves for Ericaceae and Osmundaceae. These changes match those expected during succession from open water to an ericaceous shrub association of the type which occurs on the surface today. Pollen typical of the terminal stage, a bog forest, does not replace the Ericaceae upward, but the occurrence of *Larix* and *Picea* pollen throughout zone C-3 is evidence for its presence somewhere on the bog mat. A few spruce needles recovered from the peat in the lower C-3b spectra imply the presence of spruce trees near the sampling point at the time this part of the zone was deposited. No doubt these were produced by black spruce, which is found on the bog mat today.

The C-3a/C-3b transition is abrupt and clearly marked by a decrease in AP and an increase in NAP. The largest reductions in tree pollen percentages occur in *Fagus, Pinus* haploxylon, *Quercus,* and *Tsuga. Acer saccharum* percentages drop somewhat but generally remain high, as do those for *Betula.* Only *Acer rubrum* and *Populus* show a marked increase in C-3b spectra.

At 2.5 cm beneath the surface, total NAP reaches 57 percent of the sum, the highest value reached in subzone C-3b at Allenberg Bog. Pollen from herbs, which today grow mostly in disturbed habitats, is abundant. As at the Valley Heads bogs, *Ambrosia* has higher percentages than any other NAP type. Pollen from Cheno-Ams., Cichorioideae, Gramineae *p. p., Plántago,* and *Rumex,* probably produced by weedy species, also occurs. *Fagopyrum,* Gramineae *p. p.* (incl. Cerealia), and *Zea* pollen, representing cultivated plants, is present but in much lower percentages than the weeds. Highs in the Cyperaceae, Ericaceae, high-spine Compositae, *Nemopanthus,* and Polypodiaceae curves probably reflect conditions on the bog mat favorable to the growth of local species.

Pollen Size-Frequency Measurements

Size may be a useful species character in pollen which on other morphological grounds can be identified to genus only (Cain, 1940; Cain & Cain, 1948; Leopold, 1956a). For this reason, measurements were made of as many well-preserved *Betula, Picea,* and *Pinus* diploxylon grains as possible while counting the Allenberg Bog sections. Silicone oil is a particularly effective mounting medium in such studies because gentle tapping of the cover slip rotates grains permitting access to the length chosen to be measured. The data collected have been plotted in size-frequency graphs (figures 9, 10, and 11).

Some difficulties inherent in size-frequency data have been reviewed by Whitehead (1964). The maceration procedure employed to isolate pollen from sediments, the nature of these sediments, and the medium in which the pollen is mounted for microscopic study apparently affect grain size. When these sources of variability are

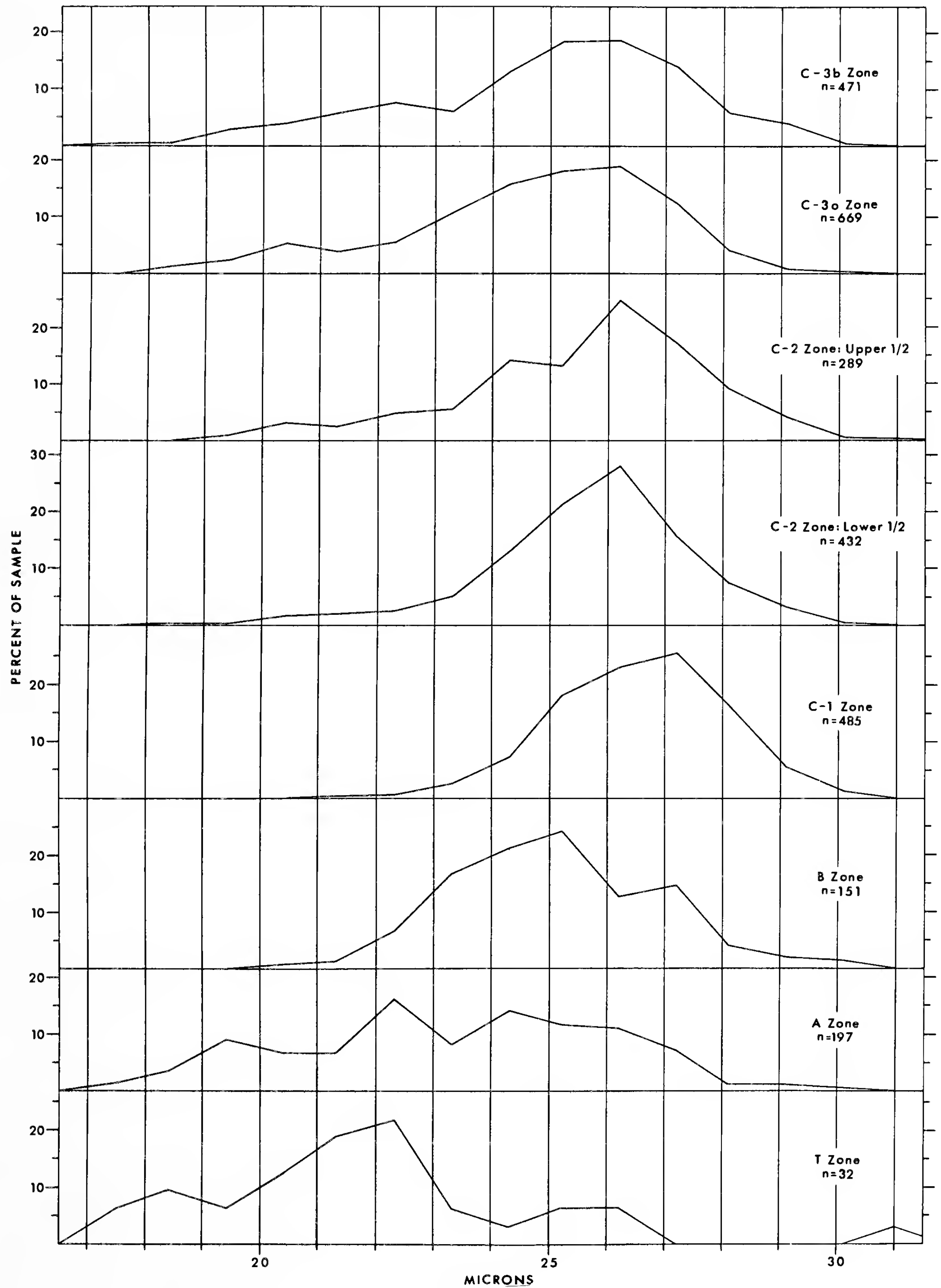

PERCENT OF SAMPLE
C-3b Zone
n=471
C-3a Zone
n=669
C-2 Zone: Upper 1/2
n=289
C-2 Zone: Lower 1/2
n=432
C-1 Zone
n=485
B Zone
n=151
A Zone
n=197
T Zone
n=32
20
25
30
MICRONS

Figure 9

coupled to the fact that in only a few cases has an analysis been made of the geographical variation in pollen size of a given species, not to mention the absence of an evaluation of differences within populations or within a single individual, fossil size-frequency data must be interpreted cautiously. However, certain of these factors have been studied and in some cases variability of pollen size is less than anticipated. For example, Faegri and Deuse (1960) exposed *Betula tortuosa* pollen to different lengths of treatment in boiling 10 percent KOH and did not find a significant size change with longer treatment, although they did observe an increase in size when acetolysis followed exposure to KOH. These authors have also shown negligible changes over a period of 5.5 years in pollen preparations mounted in water, glycerol, and glycerine jelly. Clausen (1960), who studied fresh pollen removed from different sectors of *Betula* catkins located on various parts of two birch species, was unable to demonstrate any significant size variations within a single species. Similar studies need to be extended to all species identified on size characteristics alone, but, if the same maceration procedure and mounting medium are used for the fossil samples and the modern preparations employed to identify peak frequencies within a fossil spectrum, variability caused by these factors can be minimized.

Betula. The most extensive study of size variation in pollen of the North American species of *Betula* has been published by Leopold (1956a). Birch pollen is triporate and the dimension usually measured extends from the tip of a pore across the grain to the edge of the exine in the interporal area on the opposite side. This, the maximum diameter of the grain, can be measured at three places. The grain diameter:pore depth ratio, used recently by Birks (1968) to identify *Betula nana* pollen, may also be useful in working with temperate North American species.

Measurements collected from individual spectra were lumped by zones or major portions thereof to increase sample size and to produce graphs that are characteristic of the main subdivisions of the pollen diagram (figure 9). As only one mode occurs in nearly all parts of zone C, one or possibly two birch species with pollen grains of similar size seem to have been dominant during C zone time. Today, only *Betula lenta* and *B. alleghaniensis* occur in southwestern New York State (Zenkert, 1934) and, although the former is not listed by Schick and Eaton (1963) as growing within the Allenberg Bog-Waterman Swamp area itself, it is reasonable to conclude that one or both of these species contributed most of the birch pollen to C-3b spectra. The gross volume data collected by the U.S. Forest Service show both species to be about equally abundant in Cattaraugus County (Northeastern Forest Experiment Station, 1967). Because nearly identical modes occur throughout zone C, *B. lenta* and *B. alleghaniensis* are likely to have been the only species present.

The highest size-frequencies occur over a 1 to 2 μ interval with the mode at 26 μ in zones C-3b, C-3a and the upper and lower halves of C-2. In zone C-1, however, the mode shifts to 27 μ. Leopold (1956a) has reported the mode for *Betula lenta* pollen to be 28 μ in acetolyzed samples and to be near 24 μ in those treated only with KOH. In *B. alleghaniensis,* the mode for KOH treated samples is 28 μ, but it is 45 μ for acetolyzed ones. My samples were exposed to both KOH and acetolysis, so it is expected that the modal class would be near the larger figures. The fact that they are smaller may be related to the shrinkage phenomenon reported to occur during fossilization in peat by Buell (1946), Praglowski (1966), and others. The shift in the position of the mode in zone C-1 to slightly larger grains may indicate the presence of *Betula papyrifera,* a species which, although now rare in western New York, may have been more abundant in the past.

The modes shift to smaller size classes in zone B and below. The presence of at least some grains greater than 25 μ suggests that *Betula lenta, B. alleghaniensis,* and perhaps *B. papyrifera* grew at an unspecifiable distance from the basin during the period of time represented by these zones. However, it is difficult to identify the main birch species contributing pollen to zone B sediments because none of the taxa studied by Leopold (1956a) has a mode at 25 μ. Perhaps some aspect of the depositional environment caused pollen from the three tree species to shrink more in zone B than in those zones above or possibly another species was present. If so, it may have been the shrub, *Betula pumila,* which has been found only once in western New York but may have had a wider distribution in the past. Leopold (*ibid.*) considers the pollen of this species to be smaller than that of the tree birches mentioned above, but the mode at 30 μ for the acetolyzed sample she reports does not match the mode in the fossil material. *Betula pumila* pollen treated with KOH only is smaller, however, and six samples prepared this way have a mean size of 24 μ.

The modes at 22 μ in zones A and T can be identified with more certainty. Leopold (1956a) has found

Betula glandulosa, an arctic-alpine species native as far south as the Adirondack Mountains in eastern North America (Fernald, 1950), to have small pollen with modes at 20, 22, and 23 μ in the three acetolyzed modern samples she studied. These comfortably overlap the mode for fossil grains in both zones at Allenberg Bog.

Picea. The technique of using size-frequency measurements from the surface of a deposit to interpret levels beneath can also be used for *Picea* (figure 10). There are three species of spruce that could have been members of the late and postglacial vegetation of western New York, *Picea glauca, P. mariana,* and *P. rubens.* The last named is now found mainly in mountain forests stretching from the southern Appalachians to New Brunswick and Nova Scotia (Fowells, 1965), but, in spite of some evidence that it may have occurred as far west as Michigan during the lateglacial (Cain, 1948), the distributional history of the species is largely unknown.

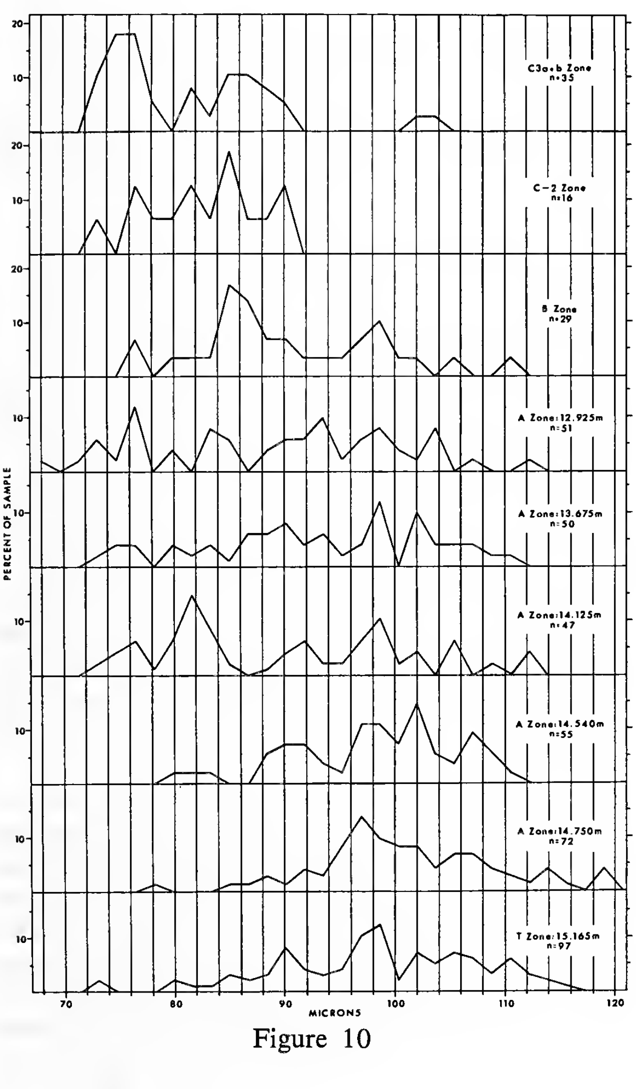


Figure 10

A number of recent workers have consistently separated the pollen of *Picea glauca* and *P. mariana.* Most use only size characteristics, but there seem also to be morphological differences between these species (*ibid.*). Size-frequency measurements indicate that the smaller grains generally belong to *P. mariana* and larger ones to *P. glauca* (Cain, *ibid.;* Davis & Goodlett, 1960; Heusser, 1960). West (1961) has used 100 μ based on wingtip-to-wingtip measurements as the point of separation between them in his work in eastern Wisconsin. Unpublished measurements of this dimension made by J. H. Anderson (personal comm.) on three collections of *P. glauca* treated with 10 percent KOH and acetolyzed have the following means: 116 μ (Arnold Arboretum, Massachusetts), 104 μ (Cheboygan County, Michigan), and 99 μ (Neultin Lake, N.W.T.). Similarly treated samples of *P. mariana* have smaller means: 85 μ (Ingham County, Michigan) and 79 μ (Thunder Bay District, Ontario). Since these data indicate that a total length greater or lesser than 100 μ is a reasonable point of division between the pollen of these species, this figure was used in the present study.

Measurements of maximum internal diameter (excluding the wings) for five collections of *Picea rubens* pollen show that the average of the means is about 3 μ greater in this species than an average of the same dimension in *P. glauca* (Davis & Goodlett, 1960). Wingtip-to-wingtip measurements are unfortunately not available for *P. rubens.*

The size-frequency graphs are readily interpreted with this information. We can be fairly certain that *Picea mariana* was the only species present in zones C-3 (including subzones b and a) and C-2 because of the probable absence of habitats for the two other species near Allenberg Bog during the past 4,000 years. Only two grains larger than 100 μ were found in these zones, and it is likely that these originated from introduced species because they occur in postsettlement spectra. As mature *Picea Abies* trees are common near farm dwellings and in cemeteries in the area, this species is a possible source. The mean grain size in the C-3a + b is 81 μ; in the C-2 it is 82 μ. Spruce pollen is practically absent in zone C-1 at Allenberg Bog. It also occurs in low percentages in the C-1 at other sites included in this study.

In zone B, the mean grain size is 91 μ and 87 percent of the grains are less than 100 μ in length. Progressively lower in the bog, the mean size becomes lar-

ger and a maximum of 101 μ is reached at 14.750 m near the bottom of zone A. At this level, 53 percent of the grains are greater than 100 μ. In zone T at 15.175 m, the mean size decreases slightly to 98 μ but 43 percent of the sample is greater than 100 μ. In zones A and T the maximum wingtip-to-wingtip length found was 120 μ. Whether such grains belong to *Picea rubens* cannot be determined, but occasional grains of *P. glauca* attain this size.

Pinus. Early work on size-frequency distributions of *Pinus* pollen suggested the feasibility of species identification on this basis. Cain (1940), for example, demonstrated three modes in a size-frequency curve of fossil pine pollen extracted from the Spartanburg buried soils on the Piedmont of western South Carolina. He related the smallest mode to *P. Banksiana* and the larger ones to *P. glabra* and *P. rigida* or *P. palustris.* In a study of pine pollen from sediments in a southeastern Michigan lake, Cain & Cain (1948) found bimodal and trimodal distributions which they considered evidence for the occurrence of *P. Banksiana, P. resinosa,* and *P. Strobus.*

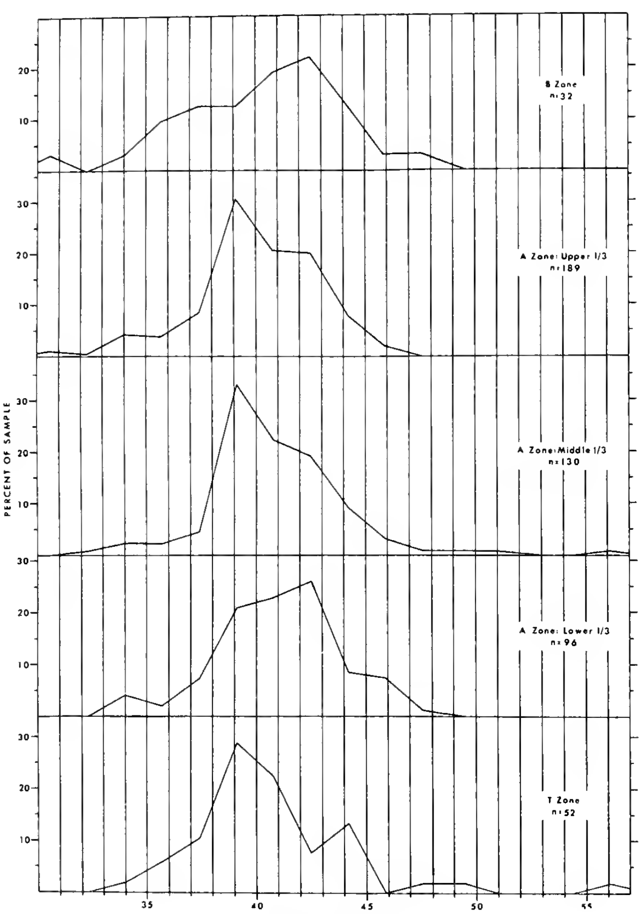


Figure 11

A simple but only recently demonstrated morphological trait, the presence of a verrucose furrow (Ueno, 1958), now allows pollen of *Pinus Strobus,* the only member of subg. Strobus in eastern North America, to be tabulated separately from smooth-furrowed pollen belonging to members of subg. Pinus. Size measurements can thus be directed at identifying the occurrence of species excluding *P. Strobus.*

Three pines with smooth-furrowed pollen, *Pinus Banksiana, P. resinosa,* and *P. rigida,* are expected in western New York pollen profiles on the basis of modern distribution patterns. Whitehead (1964) has studied pollen from all of them, and since our maceration techniques are similar, his data should be comparable to mine. Whitehead shows *P. rigida* to have the largest grains (mean size 44.95 μ based on 9 collections) and pollen of *P. Banksiana* (mean size 37.01 μ based on 24 collections) and *P. resinosa* (40.11 μ based on 12 samples) to be considerably smaller. Whitehead concludes, " it is . . . doubtful if one could separate grains of *Pinus Banksiana* and *P. resinosa* in size-frequency analysis even though the means differ by 3.10 μ . . . [and] . . . a size-frequency curve for fossil grains to which both species contributed would be perfectly unimodal " (p. 772). His measurements are of internal body diameter.

Measurements of fossil *Pinus* subg. Pinus pollen from Allenberg Bog are shown in figure 11. Since I measured external body diameter, 2 μ should be subtracted from my data to obtain figures which are equivalent to those of Whitehead (*ibid.*). In zone B, the modal class at 42.5 μ minus the 2 μ correction factor gives a figure which compares well with the mean size of *Pinus resinosa* pollen determined by Whitehead. In the upper two-thirds of zone A, the mode for the Allenberg data shifts to 39 μ (37 μ) suggesting dominance by *P. Banksiana.* A fairly prominent shoulder at 42.5 μ (40.5 μ) corresponding to the mode in the B zone also occurs in these graphs. In the lower third of zone A, the mode again shifts to the larger size class. None of my size-frequency graphs is strictly bimodal, but the correlation in size implies the presence of both species in zones A and B.

In zone T, two modes occur, one at 39 μ (37 μ) and another at 44 μ (42 μ). The lesser corresponds to the two upper A zone modes and presumably reflects the presence of *Pinus Banksiana* while the greater has no precise counterpart elsewhere in figure 11. Since the T zone was apparently a time of low pollen delivery to the basin by the regional vegetation, the probability of finding far-traveled pollen types in T zone spectra

Figure 12

is greater than elsewhere in the profile. Perhaps the higher frequency of larger grains is related to input by one of several possible pine species such as *P. rigida* which occurred at some distance south of the glacial boundary. However, no clear evidence of the presence of *P. rigida* is shown in the pre-C zone samples graphed in figure 11.

Genesee Valley Peat Works

This site occurs in an area mapped by Connally (1964) as part of the pre-Kent Olean moraine. Similarly, MacClintock and Apfel (1944) and Muller (1960) place the Kent terminal moraine north of the locality. The peat and associated sediments, which have accumulated in what seems to have been originally a shallow 10-acre lake in a pitted valley train, is being actively mined by the owner, Paul Button of Belmont, New York. The site is located in Allegany County in the Town of Amity, 2.6 mi. northeast of Belmont on the north side of NYS 244 about 0.3 mi west of Baker Valley Rd. at 42° 15′ 10″ N. lat. and 78° 59′ 37″ W. long. The surface of the peat deposit lies near the 1,620 ft contour line. The peat works is shown as an area devoid of vegetation with three small ponds marking the periphery of the peat deposit in the northwest quarter of the Wellsville North 7½′ quadrangle. The basin occurs on a flat terrace about 100 ft above Phillips Creek which flows to the southwest and empties 3 mi downstream into the Genesee River. Local relief is about 350 ft, and many of the surrounding hills reach 2,000 ft in elevation.

The peat deposit was wooded when Button purchased it in 1951, and, at this time, no outlet or inlet existed. He removed the trees and built a dike at the west end of the basin to flood it for use as a trout pond. During the ensuing years, the stumps and root mat became freed from the underlying peat and Button decided to drain the pond and excavate the peat. The surface was bulldozed clear, a channel was cut through the drift at the west end to facilitate drainage, and the peat along the south rim of the basin was removed and dragged up onto the land for drying (figure 12). Mining has continued along this edge.

According to Button, the bog surface was covered with a forest of *Acer rubrum, Betula alleghaniensis, Pinus Strobus,* and *Tsuga canadensis.* At the basin edge, *Prunus serotina* and *Ulmus* sp. occurred. Apparently *Picea mariana* and *Larix laricina* were absent. In a somewhat open area near the east end, cranberries (either *Vaccinium macrocarpon* or *V. Oxycoccos*) grew and *Arisaema* sp., *Cypripedium acaule,* and *C. Calceolus* were mentioned as noteworthy for their abundance on the forested mat.

At the present time, the site is entirely surrounded by fields or secondary forests. To the north, and contiguous with the basin margin, is a highly disturbed forest remnant, long cut over and now dominated by trees of small diameter. The following species were noted in the summer of 1967: *Acer rubrum, Crataegus* sp., *Pinus Strobus, Populus grandidentata, Prunus pensylvanica, P. serotina, Quercus alba,* and *Tsuga canadensis.* Cultivated land occurs on the east and south sides, and a plantation of small conifers in an abandoned field is located immediately to the west of the basin. In general, a large percentage of the surrounding hill tops are forested but valley floors and lower slopes are mostly fields or under cultivation. Oak-rich forests are more abundant in this area than to the west in Cattaraugus and southern Erie Counties.

Sediment Stratigraphy

The deposit was sampled on September 12, 1966, near the west end of the basin at a point where Button said that the maximum depth occurred. The Hiller borer was used from the surface to 3.25 m. The Livingstone sampler equipped with a 1-in. diameter barrel was employed beyond this depth. The stratigraphy at the sampling point is:

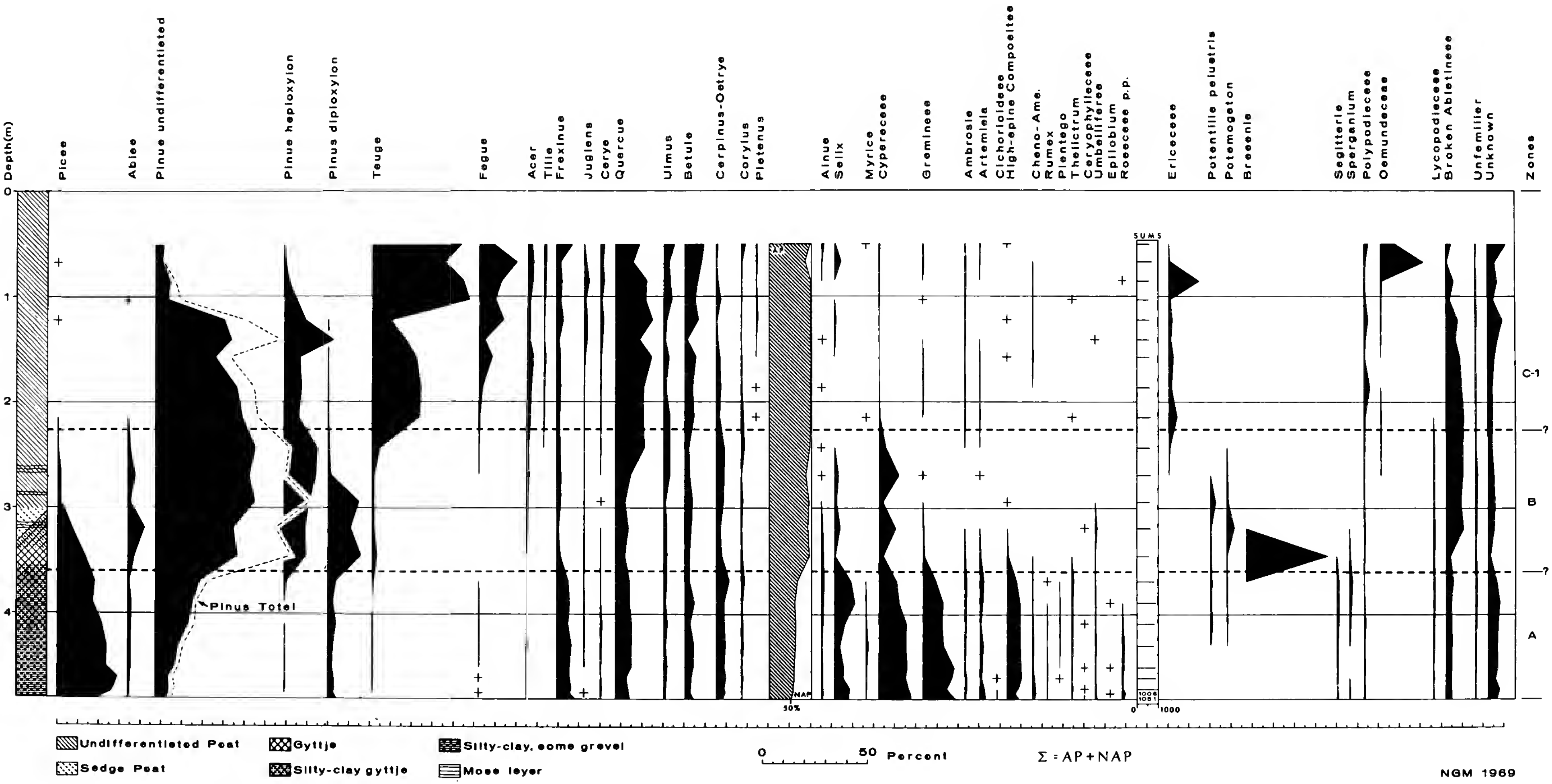
Diagram 9

Genesee Valley Peat Works: Relative Pollen Frequency

0.00–0.50 m : peat, undifferentiated, humified, dark brown, no samples taken because of disturbance;

0.50–3.00 m : peat, undifferentiated, mostly coarse near top, finer at bottom, well compacted, *Meesia trifaria* layers at 2.63 and 2.83 m, dark brown and humified at top, reddish brown commencing at 0.75 m;

GENESEE VALLEY PEAT WORKS: RELATIVE POLLEN FREQUENCY



3.00–3.25 m	:	peat, mostly sedge leaf debris, with *Meesia trifaria* layer at 3.18 m, light brown;
3.25–3.35 m	:	gyttja, brown;
3.35–4.16 m	:	gyttja, with silt and clay;
4.16–4.80 m	:	silty-clay, compact, with shale fragments and quartz sand and granules throughout but most significant near bottom, layer of gastropod shells at 4.60 m, small vivianite nodules from 4.70 m, mostly greenish gray. Further sampling not possible because of the compactness of the sediment.

Pollen Stratigraphy

The pollen zonation at the Genesee Valley Peat Works is similar to that found in the three bog deposits discussed previously. However, several important differences are apparent: the tripartite C zone does not occur, pine pollen is predominant over an exceptionally broad interval, and very high NAP percentages are associated with rather low percentages of spruce pollen in the sediments beneath zone B. These divergences from the basic pattern have made the placement of zone boundaries difficult and those shown on diagram 9 have been placed with question.

The precise age of the Olean drift on which the present site is located is unknown, but it generally is considered to be older than the Kent glaciation dated at 23,250 B.P. near Cleveland, Ohio (White, 1968). The temporal equivalence of the A and B zones at the Genesee Valley site and similar zones elsewhere in southwestern New York cannot be exact because of differences in basin age. Radiocarbon dates for all the boundaries are needed to determine precise relationships of the Genesee Valley profile.

Zone A. Spruce pollen reaches a maximum of 29 percent in one level near the bottom of the zone, but in general percentages are half what they are at the other sites in the study area. Spruce gradually decreases in abundance upward and is replaced mainly by *Pinus*. About 5 percent *Pinus* subg. Pinus pollen occurs; *Pinus* subg. Strobus pollen is only sparsely represented. Also present in A zone spectra is 2 percent *Abies* pollen.

Pollen from broadleaf deciduous trees consistently occurs in the A zone. *Fraxinus* and *Quercus* each account for about 8 percent of the sum, and lesser, but nonetheless substantial, percentages of *Betula* and *Carpinus-Ostrya* also are found. In addition, *Acer, Carya, Corylus, Fagus, Juglans, Ulmus,* and *Tsuga* pollen are present, but in very low percentages. Typically, these taxa amount to 15–20 percent of the total.

The most unusual aspect of the A zone is high percentages of NAP. In similar stratigraphic positions at the other sites, total NAP reached only 10 percent, but here it accounts for over 30 percent of the sum and reaches 48 percent in the bottom spectrum. Between 3.45 and 3.19 m, near the A/B transition, NAP decreases from 33 to 5 percent. Pollen from a variety of herbs was identified throughout zone A. Cyperaceae, Gramineae, high-spine Compositae, and *Salix* have by far the highest percentages. Total grass and sedge pollen varies from 25 to 30 percent. Lesser amounts of *Alnus, Ambrosia, Artemisia,* Cheno-Am., *Myrica, Plantago,* Rosaceae, *Thalictrum,* and Umbelliferae occur, and, of the minor types listed in diagram 9 and appendix N, the most ecologically significant are grains similar to *Empetrum* sp., *Dryas* spp., and *Saxifraga* spp., which are found in spectra below 4.5 m.

The number of pollen and spores per ml of sediment does not help to further define the A zone. Below 3.19 m, the absolute numbers vary from 42,000 per ml at 4.8 m to 85,000 at 3.45 m, with most spectra having about 50,000 grains. The increase in the number of pollen and spores upward is not great enough to overcome the decrease in spruce percentages, so similar curves are obtained whether the data are plotted on an absolute basis or not.

Zone B. The A/B zone boundary was located at the middle of the increase in the *Pinus* total curve. Greater *Pinus* percentages are compensated for by a decrease in *Picea* and nonarboreal pollen. Pollen of *Pinus* subg. Strobus and subg. Pinus are both present, and, while the former continues to occur in abundance upward, the latter falls to less than 1 percent near the middle of the zone and stays at this level until it drops completely out of the counts in zone C-1. In some spectra, total *Pinus* accounts for 70 percent of the sum. *Abies* percentages reach a peak just below the middle of zone B.

High percentages of *Quercus* pollen which occur with pine in zone B at the other sites are not present until near the end of the zone. In the bottom half of zone B, *Quercus* is found in slightly lower percentages than were present throughout zone A, but above the middle of zone B, *Quercus* increases from 7 to about 15 percent.

The B/C-1 boundary was placed at the middle of the interval where total *Pinus* percentages decrease and *Tsuga* percentages reciprocally increase. The abrupt

rise in the *Tsuga* curve marks the beginning of zone C-1 at this site as at others in southwestern New York. A slight increase in percentages of *Ulmus* and *Carpinus-Ostrya* is apparent near the ènd of zone B, but percentages of other AP types remain fairly constant across the zone.

NAP percentages in zone B are about one-fourth of lower spectra. Cyperaceae and *Salix* pollen are the two most abundant types.

Intrabasinal succession is well defined by peak pollen frequencies of bog and lake indicator species at various levels in the sediments which themselves are evidence for such change. Pollen from *Sagittaria* and *Sparganium*, two shallow water, near-strand aquatics, occur in the lowest spectrum and upward for over 1.5 m. They imply that the water was probably too deep during most of this interval to permit other aquatics to grow near the sampling point. Somewhat higher in the sediments, *Potamogeton* makes its first appearance, and later *Brasenia* occurs in abundance. These are rooted, open water aquatics which generally grow in shallow ponds. Both have peak frequencies higher in the section, near the level where *Sagittaria* and *Sparganium* drop out of the counts. *Potentilla palustris* and *Potamogeton* first appear together, but the peak percentage of the former is slightly above that of the latter, a situation perhaps caused by the occurrence of *Potentilla palustris* at the leading edge of an advancing bog mat. High percentages of Cyperaceae pollen occur in these levels and in those immediately above, at which point both *Potentilla* and *Potamogeton* have nearly dropped out of the counts. The Cyperaceae high occurs precisely between the last occurrence of *Potentilla palustris* and the first occurrence of Ericaceae pollen. In absolute numbers of pollen per ml of sediment, sedge pollen is more than twice as abundant in this part of the profile than in the A zone. Within this interval occur three separate horizons of the moss *Meesia trifaria*, a predominantly boreal forest species with disjunct stations throughout the Great Lakes states. It grows in bogs and swampy woods, often in somewhat calcareous situations. Upward, Cyperaceae percentages decrease and percentages of Ericaceae and Polypodiaceae rise. Ericaceae reach a peak near the top of the profile, and, slightly above this, maximum Osmundaceae percentages occur.

These changes record the presence of several distinct plant communities which probably occurred largely in response to the degree of basin infilling. In a developmental sequence, open water, sedge mat, ericaceous shrub heath, and bog forest are the main ones indicated. The bog forest is the least clearly defined, but evidence of its presence is afforded by high percentages of Osmundaceae spores similar to those produced by *Osmunda cinnamomea* and *O. regalis*, species characteristic of this habitat.

Zone C. The entire C zone is truncated and no subdivisions as defined in previous profiles can be discerned. *Tsuga* and *Fagus* pollen curves indicate that only zone C-1 is present. The *Tsuga* curve is unparalleled elsewhere in the study area. High *Pinus* percentages persist well above the B/C-1 boundary, and *Pinus* subg. Strobus pollen is the predominant type present. Between 0.5 and 1 m, *Pinus* drops below 10 percent of the total.

Pollen from deciduous tree species show a gradual increase in the upper C-1 spectra. *Acer, Betula, Carya, Fagus, Fraxinus, Juglans, Tilia,* and *Ulmus* have higher percentages at the end of the zone than at the beginning. The temporary decrease in the *Betula, Fagus,* and *Quercus* curves at 1.41 m is associated with a reciprocal increase in *Pinus*. This probably reflects a short term change during which *Pinus* became more abundant locally, perhaps due to disturbance.

Total NAP percentages are low and account for less than 2 percent of the sum in all C-1 spectra except at 0.67 m where *Nemopanthus, Rhus, Salix,* and *Viburnum* pollen, probably from species growing on the bog mat, account for over 12 percent of the sum.

Interpretation

ZONE T

Among the sites included in this study, pre-A zone spectra with total NAP amounting to 50 percent or more of the sum occur only at Allenberg Bog, although the lowest spectra from the two Valley Heads bogs contain enough nonarboreal pollen to indicate they are transitional between the NAP-rich T zone and the comparatively NAP-poor A zone. The large nonarboreal pollen content in what I have called the A zone at the Genesee Valley Peat Works is difficult to interpret and will be discussed under zone A. Herb-rich pollen spectra have been reported previously from two sites in upstate New York: Crusoe Lake near Syracuse (Cox & Lewis, 1965) and Kernochan Bog southwest of the Catskill Mountains near the Pennsylvania border (Stingelin, 1965). Erratic fluctuations of tree and herb pollen percentages in the basal gravelly clay at Crusoe Lake and then unknown age of the sediments make interpretation difficult, but the authors tentatively suggest correlation with the Port Huron (Mankato)–Two Creeks–Valders sequence recognized in pollen diagrams from northern Maine (Deevey, 1951). At Kernochan Bog, from 15 to 45 percent NAP occurs in a 2.5 m section of silty clay differentiated as zone T. The entire interval is taken as evidence of a period during which the vegetation near the site was taiga-like. It is of interest that *Quercus* pollen is nearly absent from the bottom 1.5 m of zone T at Kernochan Bog.

T zones, or Herb Pollen Zones as they have come to be called more recently, have otherwise been found in various parts of glaciated eastern North America (Davis, 1967a; Sirkin, 1967), Michigan (Andersen, 1954), Minnesota (Cushing, 1967), and elsewhere. Zone T pollen assemblages from Allenberg Bog have much in common with comparable spectra from these regions, but, in general, sites in New England have less spruce and more sedge pollen, while at Minnesota and Wisconsin localities, more spruce but about the same percentage of sedge pollen occurs.

In recent years, pollen diagrams have been most effectively interpreted by relating the pollen rain in regions of known vegetation to fossil pollen spectra. If fossil and modern pollen assemblages are similar, a high probability exists that the vegetation producing them was analogous, and, as an extension of this, it can be further reasoned that the climate controlling the vegetation was similar at both points in time. The pollen content of uppermost lake sediments, moss polsters, and other surficial pollen traps has been determined at many localities across northern North America.

Among the surface counts compiled by Davis (1967a), none is exactly like zone T pollen assemblages at Allenberg Bog, although certain spectra from tundra and boreal forest regions of Laborador are more or less similar. The pollen rain in the boreal forest-tundra ecotone at Fort Churchill, Manitoba (Ritchie & Lichti-Federovich, 1967) also more or less resembles Allenberg Bog T zone pollen assemblages. Major pollen types found at the surface at Fort Churchill include *Picea* (13 percent), *Pinus* (25 percent), *Betula* (11 percent), Gramineae (6 percent), and Cyperaceae (24 percent). Lesser amounts of *Larix, Alnus, Salix, Myrica,* and pollen of a number of herbaceous species are also present. At this particular site, only 0.1 percent *Artemisia* pollen occurs (*vs.* 5 to 8 percent at Allenberg Bog), but at other sampling localities in the same vegetation type, up to 17 percent is present. The vegetation near Fort Churchill today appears to be a fairly close analogue to that which existed near Allenberg Bog during accumulation of zone T sediments, although as Davis (1967a) points out, the current pollen rain in the tundra and tundra-forest ecotone is too similar to permit distinguishing these vegetation types in the fossil record.

The density of trees across the landscape near Allenberg Bog during zone T time is difficult to estimate. Pollen of *Picea* (20 percent) and *Pinus* (10 percent) indicates that spruce and pine grew within pollen dispersal distance but not necessarily close to the basin. For example, Ritchie and Lichti-Federovich (1967) report 4 to 35 percent spruce pollen from various parts of subarctic Canada where spruce trees occur in widely scattered stands surrounded by extensive heaths and dwarf-birch tundra. Hafsten (1961), working in the southwestern United States, found pine pollen (up to 10 percent) 150 mi from its nearest source, and over 10 percent has been reported from surfaces at three high-

arctic sites (Ritchie & Lichti-Federovich, 1967). As these findings indicate, pine and spruce pollen can be blown into areas where the parent plants either do not occur or are of patchy distribution.

Among other arboreal pollen types identified in zone A, those of thermophilic, Temperate Zone genera and species are anomalous in a pollen assemblage which otherwise indicates the vegetation surrounding the site was similar to that in the boreal forest-tundra ecotone. These include *Fraxinus nigra* (from 3 to 5 percent), *Quercus* (from 3 to 8 percent), and a few grains (2 percent and less) of *Carpinus-Ostrya, Carya, Corylus, Fraxinus americana* and/or *F. pennsylvanica, Juglans cinerea,* and *Ulmus.* Such pollen frequently occurs in late glacial T and A zone spectra throughout glaciated eastern North America. Its presence has been explained by claiming redeposition from older sediments (Andersen, 1954) and long-distance wind transport (Deevey, 1951). For climatic reasons, a third alternative, that species producing these types actually grew nearby, seems less likely, at least during accumulation of zone T sediments.

No source near Allenberg Bog for rebedded pollen is known. Pollen in zone T at this site is extremely well preserved and shows little evidence of abrasion. However, a strong case can be made for wind transport using data published by Ritchie and Lichti-Federovich (1967) who measured the pollen rain at Fort Churchill for 6 days in early May, a time when local plants had not begun to flower. During each 24-hour period at least one *Quercus* grain was trapped and a maximum of four grains was collected on one of the 6 days. Other types were recovered less frequently, but were often more abundant. For example, pollen of *Ulmus* (17 grains), *Corylus* (15 grains), *Fraxinus* (5 grains; pollen with three and four colpi not separated) were trapped in one 24-hour period. All anomalous pollen types occurring in zone T at Allenberg Bog except *Carpinus-Ostrya* were found capable of being carried to Fort Churchill from sources 500 to 1000 mi away. Furthermore, because absolute pollen frequency data indicate a low delivery rate of pollen and spores to basins during the T zone interval, the area contributing to the pollen rain may have been much larger at this time than during any subsequent period. Fewer than 1000 grains/cm^2/year were deposited during the T zone interval at Rogers Lake, Connecticut, in sediments older than 12,000 B.P. (Davis, 1967b). The absence of radiocarbon dates from Allenberg Bog makes similar calculations impossible, but the number of grains/ml of sediment is nearly equal in pre-A zone spectra at both sites. With a relatively small number of grains reaching a basin every year, the few grains occasionally shed in the air by local entomophilous species and those derived from distant sources would have an increased chance of being expressed in pollen counts. This also is borne out by data from Fort Churchill where a deposition rate of 1400 grains/cm^2/year has been measured and pollen from both entomophilous taxa and distant trees occur (Ritchie & Lichti-Federovich, 1967).

Calculated as a percent of the sum of all other trapped pollen and spores, however, pollen of Temperate Zone tree species at Fort Churchill amounts to only 0.6 percent of the total. Since higher percentages of *Quercus* and *Fraxinus* pollen occur at Allenberg Bog, species of oak and ash perhaps grew much closer to the site than did species of *Carya, Corylus, Juglans,* and *Ulmus.* The nearness of Allenberg Bog to the unglaciated Salamanca reentrant and other ice-free areas further south suggests that black ash and at least one species of oak may have occupied favorable habitats some tens of miles beyond the terminal moraine. Of the ashes in eastern North America, *Fraxinus nigra* currently has the most northern distribution, so it seems likely that individuals may have been able to survive fairly close to the ice front. Similarly, *Quercus macrocarpa* and *Q. rubra,* which occur northward to the edge of the boreal forest, are the most probable members of the late glacial T zone vegetation near Allenberg Bog.

Davis (1958) has pointed out that T zone herb pollen assemblages are mixtures of taxa which have both northern and southern affinities. Allenberg Bog samples yield pollen of *Artemisia,* Caryophyllaceae, Rosaceae, *Ranunculus, Salix,* Cichorioideae, and Asteroideae (= high-spine Compositae *p. p.*), all of which have species in both arctic and temperate regions. Other pollen types identified in T zone sediments are from taxa which are mainly temperate in distribution. At Allenberg Bog these include *Ambrosia,* Chenopodiaceae-Amaranthaceae, Labiatae, and Umbelliferae. Taxa found exclusively in arctic and subarctic regions have not been identified in the basal layers at Allenberg Bog. However, the presence of *Betula glandulosa* is indicated by size-frequency measurements of *Betula* pollen. This birch is an arctic-alpine species which today is widespread in the North American subarctic and extends southward in eastern North America to the Adirondack Mountains (Fernald, 1950). Microspores of *Selaginella selaginoides,* a species that grows at exposed calcareous sites in boreal forest and subarctic regions across North America as far south as the upper Great Lakes and northern Maine (*ibid.*), are found also in zone T sedi-

ments at Allenberg Bog. The presence of these species and pollen from other taxa with high light requirements, supports an interpretation involving the existence of an open or semiopen tundra-like vegetation.

In the absence of radiocarbon dates, it cannot be determined if the semitreeless landscape which occurred adjacent to Allenberg Bog was a successional stage transitional to a spruce forest, or whether a climatically-controlled group of communities equivalent to several of the many expressions of tundra vegetation was present. In southern New England, where tundra persisted several millenia prior to 12,000 B.P. (Davis, 1967b), the treeless interval probably represents a period during which the climate was too severe to allow the development of spruce forest, although trees may also have been absent because they had not migrated to the region.

To summarize, Allenberg Bog T zone pollen assemblages seem clearly to imply the occurrence of park-tundra vegetation prior to development of A zone spruce communities. Size-frequency measurements indicate that *Picea glauca* was the main species of spruce present, although *P. mariana* undoubtedly occurred to some extent also. Spruce trees may have been sparsely scattered across the landscape or occurred some tens of miles away. Also present were *Pinus Banksiana* and/or *P. resinosa,* although these species may have grown far south of the site because pine pollen in the amount present may result from long-distance transport. Plant communities rich in sedges, grasses, and heliophytic herbs probably dominated much of the region. Apparently, few true tundra species were present, although a dwarf birch, *Betula glandulosa,* and *Selaginella Selaginoides,* both of which are northern in distribution, are represented in the deposit.

ZONE A

One of the most consistent stratigraphic features in basal lake and bog sediments across glaciated eastern North America is a zone in which spruce pollen accounts for 30 to 70 percent of the sum. In New York State, the presence of a spruce or A zone was early established by McCulloch (1939) from a bog near Syracuse, and other workers have since demonstrated similar zones from sedimentary basins throughout central and eastern New York (Cox, 1959; Durkee, 1960). A zone rich in spruce pollen also occurs at the four sites in southwestern New York I studied, but because the zone differs from basin to basin, it will be discussed in reference to each of the localities.

Genesee Valley Peat Works

Low spruce percentages and high values for total NAP set zone A at the Genesee Valley Peat Works apart from the others. Most A zone spectra at this locality contain less than 25 percent spruce pollen, although a maximum of 29 percent occurs at one level. By comparison, from 40 to 65 percent is present in equivalent stratigraphic positions at the three other sites. Associated with spruce pollen at the Peat Works are unusually high percentages of Cyperaceae, Gramineae, high-spine Compositae, *Salix,* and other NAP types. Replotting A zone spectra on an absolute basis does not greatly change the form of the curves. Although the overall pollen stratigraphy of the entire diagram is basically similar to the other profiles from the region, the unusual character of the spruce zone makes its interpretation difficult.

Nearly equal representation of AP and NAP throughout zone A at the Peat Works, and particularly near the bottom where *Pinus* percentages are low, implies that the regional vegetation was open and perhaps similar to that which occurred near Allenberg Bog while pre-A zone sediments accumulated there. Somewhat larger spruce percentages in the lower part of the zone may indicate that spruce trees were more abundant around the site early in the depositional history of the basin. Pine pollen increases at the expense of spruce higher in zone A, suggesting that pines became more frequent in the surrounding vegetation with the passage of time. *Pinus Banksiana* and/or *P. resinosa* seem to have been the only species present because *P. Strobus* pollen is only sparsely represented. However, because at least some pine pollen could have been blown in from a distance, the actual abundance of pine in the vegetation around the site must remain conjectural for the lowest part of the profile.

A climate too cold to permit development of more dense spruce and pine communities may have been the controlling factor in the lower part of zone A where pollen identified as *Dryas* sp., *Empetrum nigrum,* and *Saxifraga* sp. is found. The proximity of an ice front may have induced conditions favorable for tundra communities and at the same time might have kept *Picea* from becoming more abundant across the landscape. High frequencies of sedge, grass, and forb pollen are expected in vegetation of this type. A warming trend that aided the colonization of the region by *Pinus Banksiana* and/or *P. resinosa* may have occurred in the upper 1.25 m of zone A. The NAP contribution remains more or less constant during this interval implying persistence of open vegetation.

Incomplete knowledge of the current pollen rain in many sections of northern North America hampers search for a modern analogue of the A zone vegetation near the Peat Works. If pollen spectra from this zone truly represent the regional pollen rain, they cannot be matched with any of the surface samples reviewed by Davis (1967a) because modern pollen assemblages in which *Carpinus-Ostrya, Fraxinus, Quercus,* and *Ulmus* pollen are minor but significant components of spectra otherwise dominated by *Picea, Pinus,* and NAP are unknown. The possibility of a southern source for pollen of these predominantly Temperate Zone genera has already been discussed.

Since the Peat Works is situated on Tazewell or pre-Tazewell Olean drift (Muller, 1965), the lowest part of the profile may antedate most other pollen records in eastern North America. Parallel data are not present at other sites investigated in southwestern New York because they had their inception following subsequent glacial advances. Elsewhere in eastern North America, however, several deposits on Olean drift have been studied previously. Highland Lake south of the Catskill Mountains (Cox, 1959) is truncated basally due to incomplete sampling, as is the Cranberry Bog profile from eastern Pennsylvania (see Stingelin, 1965; Gehris, 1965), but the long sedimentary record at Kernochan Bog (Stingelin, 1965), located near Highland Lake about 150 mi east of central Allegany County, contains spectra roughly similar to those at the Peat Works. At Kernochan Bog, below a point where spruce reaches the A zone maximum (35 percent), there is a long, undated interval of lower spruce percentages and high *Pinus* values which does not occur at the Peat Works. Although total NAP values at Kernochan Bog are less than those at the Peat Works, the pine and spruce curves at both sites are essentially identical above the maxima, which suggests these spectra may have regional significance. This may indicate that for an unknown period following Tazewell(?) glaciation and perhaps contemporaneous with subsequent ice advances, a more or less open park-tundra or a sparse spruce-pine woodland existed on the Allegheny Plateau of southern New York and adjacent regions. Pollen analyses of sediments from unglaciated southeastern Pennsylvania below a radiocarbon date of 13,360 ± 230 B.P. (Y-479; Martin, 1958b) have produced spectra somewhat similar to zone A samples at the Genesee Valley Peat Works, but the contemporaneity of the deposits cannot be proved because the age of the Peat Work's sediment is not known. At the Pennsylvania locality, the main differences include larger total NAP percentages (50 to 75 percent) and a weaker expression of *Picea* (ca. 5 percent); *Pinus* comprises from 15 to 25 percent of the total. In light of the uncertain age of the various drift sheets east of the Salamanca reentrant, and of the Genesee Valley and Kernochan Bog pollen profiles, and in the absence of radiocarbon-dated profiles between these two localities, the park-tundra hypothesis is presented as one of several explanations of existing data.

If, however, the NAP was derived mainly from a source near the basin, an alternate interpretation is possible. In this case, the regional vegetation contributing pollen to A zone sediments at the Peat Works may not have been an open park-tundra, but perhaps a more dense spruce-pine woodland, possibly equivalent to zone A vegetation at Allenberg, Houghton, and Protection bogs. As a correction for possible local overrepresentation, A zone pollen percentages can be recalculated eliminating NAP from the counts and using the total number of arboreal pollen at a given level for the percentage base rather than the sum of AP and NAP. The new curves will show the same trends because total NAP is more or less constant throughout the interval. However, the percentage of major arboreal components in the counts increases, and spruce, for example, attains a maximum of nearly 50 percent. The overall transition from the Spruce-dominated basal sediments to pine-dominated sediments above is not unlike the A/B zone transition at other sites in western New York with the exception that it is more gradual.

Several lines of evidence point toward the possibility of local overrepresentation. The slopes above and leading to the center of the basin are gentle and the depression itself is large and relatively shallow. Therefore, an abundance of habitats for marsh plants could have existed around the margin of the basin during its early history. The presence of *Sagittaria* and *Sparganium* pollen throughout zone A indicates that marshy shallows existed at or near the basin. Both genera are not represented in counts higher in the deposit, perhaps because littoral habitats were eliminated by development of a bog mat. While other parts of the valley floor on which the depression is located may have supported marsh communities also, bedrock highs are abundant in the area and well-drained upland sites must have been a regular feature of the landscape.

The spectra may also be contaminated by redeposited pollen. I have not demonstrated that rebedding has occurred since a source of older pollen is unknown in the area, but presence of *Fagus* pollen in the silty clay at the bottom of the deposit and its absence from the more organic sediment immediately above suggest that pollen

eroded from nearby drift may have been carried to the basin with inorganic sediment. Andersen (1954) has asserted that the optimum time for redeposition is during an ice advance when frost activity would be continuously exposing potential pollen-bearing deposits. The occurrence of *Fagus* grains together with pollen of *Dryas, Empetrum,* and *Saxifraga* might be explained by claiming a climate favorable for solifluction. Since there is no objective way to determine what part of a pollen spectrum is composed of redeposited pollen or pollen from local, onsite sources, modified spectra, which might compare more favorable with one or more of the surface pollen assemblages now known, cannot be obtained.

Allenberg Bog

At this site, zone A overlies an interval which I interpret as a record of a more or less treeless landscape with herb communities covering much of the region near the basin. Above this, a rapid increase of spruce percentages occurs and high spruce values are maintained for about 2 m of sediment. Fluctuations in relative numbers of subdominant AP types, however, allow the interval to be divided into several subzones reminiscent of those reported from southern New England (Leopold, 1956b; Leopold & Scott, 1958; Davis, 1958). The correspondence of the subzones in the two areas is not exact, and percentage changes in the Allenberg Bog profile are poor evidence of modification of forest composition induced by advance and withdrawal of an ice sheet.

Four divisions of zone A are recognized at sites studied by Davis (1958) in southern New England. At Tom Swamp, Massachusetts, the *Picea* curve increases in the lowest subzone (A-1), while *Pinus* values decrease slightly over the same interval. These changes are also present across a comparable stratigraphic interval in the Allenberg Bog profile. However, high values for *Betula* and *Populus* pollen (ca. 10 percent each) which characterize subzone A-1 at Tom Swamp are absent from Allenberg Bog, and without other stratigraphic markers, an A-1 cannot be defined readily at Allenberg Bog. At Tom Swamp, *Betula* and *Populus* values drop to 5 percent or less of the total in the next highest subzone (A-2), and a pronounced maximum of relative numbers of *Picea* pollen is present also. Somewhat lower *Quercus* percentages occur in this subzone than are present in the A-1 or in the A-3 above. At Allenberg Bog, a spruce peak occurs between 14.70 and 14.94 m, but in contrast to the New England locality, maximum percentages of *Quercus* and *Fraxinus nigra* pollen also occur in this interval. The Allenberg *Quercus* curve shows no important fluctuations below the *Picea* peak, but the maximum A zone percentage of *Fraxinus nigra* pollen occurs just beneath it. Subzone A-3 at Tom Swamp has somewhat lower *Picea* percentages and increased values for *Pinus, Quercus,* and other AP types. At Allenberg Bog spectra between 14.22 and 14.70 m can be assigned to subzone A-3. Higher percentages of *Carpinus-Ostrya* occur in this interval than elsewhere in zone A, although a maximum for this pollen type is reached just above the *Picea* peak. Spruce percentages increase in subzone A-4 which, at Allenberg Bog, occurs in the upper two-thirds of zone A between 12.80 and 14.22 m. *Pinus* values are lower at the middle of A-4 than in A-3, but the curve of the sum of the three pine categories increases gradually across the upper part of A-4. In contrast to the New England diagrams, *Carpinus-Ostrya, Fraxinus nigra,* and *Quercus* percentages do not decline in A-4.

Interpretation of the New England A zone sequence has been related to late Wisconsin glacial events (see Beetham & Niering, 1961; Davis, 1965b). For example, the climate following retreat of Port Huron ice presumably improved, permitting spruce to increase and attain maximum abundance (subzones A-1 and A-2). Lower relative numbers of *Picea* and increased percentages of *Pinus* and deciduous tree pollen types implied further warming during the A-3. Several radiocarbon age determinations permitted initial correlation of the A-3 with the Two Creeks Interstade (see Leopold, 1956b). A return to higher spruce percentages and a drop in oak and pine values in the A-4 were taken as a record of a spruce-dominated forest developing in response to colder climate thought to have prevailed during the ensuing Valders Stade. However, recent dating of the Two Creeks forest at 11,850 ± 140 B.P. (Broecker & Farrand, 1963) makes its correlation with the New England A-3 doubtful.

The similarity between the Allenberg Bog profile and certain New England pollen diagrams may be fortuitous. The lower part of zone A at Allenberg Bog is perhaps not temporally equivalent to spectra with comparable pollen assemblages in diagrams from New England. Accepting 23,250 B.P. (White, 1968) as the age of the Kent drift upon which Allenberg Bog is situated, not only Valders-Two Creeks climatic changes may have influenced the vegetation surrounding the site, but also those associated with the preceding Cary and Port Huron glaciations. Records of these events in the pollen profile may be in part preserved beneath zone A lower in the incompletely sampled clay deposit, but the A zone itself seems not to show any well-defined

changes that might be related to them. At Houghton Bog, 25 mi northeast of Allenberg Bog, wood from near the bottom of zone A is of Two Creeks age (11,880 ± 730 B.P., I-3290). The sample occurs with *Picea*-dominated pollen spectra which are similar to those in the upper part of zone A at Allenberg Bog. Between the dated level and the end of the spruce zone at Houghton Bog, which encompasses the time of the Valders readvance, changes in pollen percentages similar to those just reviewed from southern New England profiles do not occur. Vegetation in southwestern New York State does not seem to have been affected by climatic changes accompanying the Valders readvance. The maximum southward extension of Valders ice was more than 100 mi north of southwestern New York, apparently never reaching the Lake Ontario basin (Karrow *et al.,* 1961) which was then occupied by Glacial Lake Iroquois.

Replotting section C of the Allenberg Bog profile on an absolute basis permits a different approach to interpretation of the A zone sequence (cf. diagrams 7 and 8). Variations in absolute numbers of different pollen types per unit volume of sediment through time are meaningful, however, only if the sedimentation rate was more or less constant across the interval being considered. Although changes in pollen deposition rates are useful data for assessing vegetation change, if sediment accumulation is constant, variations in absolute numbers of types of pollen with depth will show the same trends. The sedimentation rate at Allenberg Bog should be determined by C-14 dating as has been done at Rogers Lake where, between 14,000 and 10,000 B.P., a more or less constant rate of 0.037 cm/year has been measured (Davis, 1967b; cf. Davis & Deevey, 1964).

In the absence of the necessary age determinations, however, the following paragraph is based on the assumption that the time taken to accumulate a unit volume of sediment was the same in all divisions of zone A.

At Allenberg Bog across the interval in which A zone percentages of *Quercus* and *Fraxinus nigra* pollen are high, the number of grains per ml of sediment increases (figure 8). Between 14.540 and 14.425 m, the pollen and spore total stabilizes near 200,000 grains per ml where it remains until the end of zone A. The increase probably is due mostly to a greater number of spruce and pine pollen being deposited in the basin and this may indicate an increase in the number of spruce and pine trees in the region. By 14.425 m, the maximum attainable density of spruce-pine forest may have been reached, and, above this level, no important changes are evident in *Quercus* and *Fraxinus nigra* percentages. Higher relative pollen frequencies just above the T/A zone boundary may reflect the openness of the developing spruce forest when fewer numbers of *Picea* pollen relative to *Quercus* pollen were being deposited. If the input of *Quercus* remained constant, as was the case according to diagram 8, an increase in the absolute numbers of spruce and pine pollen being deposited would reduce percentage values for *Quercus.*

A similar situation prevails at Rogers Lake where zone A begins at 12,000 B.P. and ends about 9,500 B.P. (Davis, 1967b). *Quercus* pollen is present during the entire interval, but 10,500 years ago it fell from about 15 to 5 percent. Less pronounced reductions also occur in *Carpinus-Ostrya* and *Fraxinus* curves at this site. These changes, clearly expressed in the relative frequency diagram, are not maintained when the data are converted to numbers of pollen and spores accumulating per unit area per year. The pollen input from *Quercus* and other temperate deciduous trees remains relatively constant during the entire interval, and the maximum and minimum of oak pollen at 11,000 and 10,000 years, respectively, that occur in the percentage diagram, no longer exist. Davis (*ibid.*) concludes that fluctuations of *Quercus* percentages reflect increasing deposition rates for coniferous tree pollen 10,000 years ago, not a climatic oscillation correlated with the Allerod–Younger *Dryas* sequence.

Upper A zone spectra at Allenberg Bog, with the exception of somewhat higher percentages of *Carpinus-Ostrya* and *Fraxinus,* agree fairly well with southern New England spectra from equivalent stratigraphic positions. Davis (1967a) considers the New England fossil pollen assemblages to be similar to surface samples deposited today in the Nichicun Lake area west of Schefferville, Quebec (ca. 53° N. lat.). This region has been characterized as an open, park-like woodland in which closed black spruce forests, with an admixture of larch, are present at wet lowland localities while black and white spruce and balsam fir occur in open stands interspersed with lichen communities on the better drained, upland sites (Terasmae & Mott, 1965). Davis (1967a) suggests that the lower part of the New England A zone represents tundra-forest transitional vegetation which developed into a boreal woodland later in the zone. Such a change is evidence of gradual climatic warming. The data from Allenberg Bog would seem to fit this interpretation, but it is to be treated as tentative until confirmatory information is obtained from other sites in southwestern New York State.

The gradual increase in the number of *Quercus* grains in the sediment from zone T to the beginning of zone A may represent northward migration of oaks to posi-

tions nearer the basin. The occurrence of from 5 to 7 percent oak pollen throughout the upper part of zone A may indicate that oaks were present somewhere within 100 mi or less of the bog. *Quercus* percentages of this magnitude have not been calculated for sites in the boreal forest or in the more open subarctic woodland to the north, either of which, on other evidence, is the closest analogue of the A zone vegetation. In eastern North America near the northern distributional limit of the genus (ca. 46° N. lat.), similar percentages occur. But since this is located in the mixed coniferous-deciduous forest of mid-Ontario, significant percentages of *Acer*, *Ulmus*, and other temperate AP types are present also. These are present in zone A at Allenberg Bog, but in much lower amounts. Less than 1 percent *Quercus* pollen, calculated using the sum AP as the percentage base, was found by King and Kapp (1963) at the southern edge of the boreal forest north of Georgian Bay.

A relatively high representation of temperate tree pollen in existing vegetation dominated by spruce and larch has been found by Janssen (1967) at Myrtle Lake on the Lake Agassiz plain of north-central Minnesota. By comparing an estimate of the original forest composition derived from the General Land Office Survey notes with pollen deposited on the surface at a number of points along transects at the lake, he showed *Picea* and *Larix* to have high importance values in the surrounding vegetation, but to be relatively poorly represented in surface pollen spectra. On the other hand, *Fraxinus, Quercus,* and *Ulmus* pollen were distinctly overrepresented in reference to the regional vegetation. If spruce and larch had a similarly low " delivery capacity " during late glacial time, they would be underrepresented in pollen profiles while higher percentages for certain extra-regional deciduous trees with greater "delivery capacity" would be expected in spite of the probability that they composed only a minor part of the regional vegetation. This situation may apply to A zone pollen assemblages at Allenberg Bog.

Using 100 μ as the dividing point between the smaller pollen of *Picea mariana* and the larger *P. glauca* grains, size-frequency measurements of A zone spruce pollen at Allenberg Bog confirm the presence of both species (figure 10). *Picea rubens* may or may not have been present also. At 14.750 m near the bottom of the zone, the mean size of measured spruce grains was 101 μ; wingtip-to-wingtip measurements were greater than 100 μ in 53 percent of the sample. Higher in the profile, the mean size decreases. Near the end of the zone at 12.925 m, it is 89.2 μ and only 17.6 percent of the measured sample was over 100 μ. Gradual loss of *P. glauca* upward and, probably, replacement by *P. mariana* is implied.

Most of the pine pollen in the Allenberg A zone is the *Pinus* subg. Pinus type. The configuration of the modes in the size-frequency curves for this pollen type (figure 11) may indicate that both *Pinus Banksiana* and *P. resinosa* contributed to zone A sediments. In view of the similarity in pollen size of these species (Whitehead, 1964), however, conclusive identification of species is not possible. The occurrence of about 20 percent of pine pollen throughout the zone definitely establishes that one or both of these pines grew near the basin. This is in contrast to the situation in the western Great Lakes region where significant amounts of pine pollen are not found in the profile until near the end or following the spruce zone (Wright, 1964, 1968b). Judging from the present day habitat preferences, both *P. Banksiana* and *P. resinosa* grew on dry sandy soils, although the former was probably restricted to the driest sites. The low relative frequency of *Pinus* subg. Strobus pollen indicates that *P. Strobus* was not a part of the regional vegetation because the relatively small amount of white pine pollen present in the counts could have been blown to the basin from afar.

The broad size class spread and the occurrence of several modes in the A zone size-frequency curve of *Betula* pollen indicates that more than one species was present near Allenberg Bog (figure 9). The smallest grains, 20 μ or less, may have been produced by the arctic-alpine dwarf birch, *B. glandulosa.* This species was apparently also present during accumulation of underlying T zone sediments. The modal classes centering near 22 and 24 μ, however, have no exact counterparts among the nine out of eleven native northeastern North American birches studied by Leopold (1956a). Although it could be postulated that extinct species contributed to the modal classes, it is more likely that the maceration technique or some aspect of the depositional environment modified grain size. In the upper part of zone C, for example, where the principal contributors to the pollen rain were *B. lenta* and *B. alleghaniensis,* the modal class is smaller than that reported for pollen from herbarium specimens of either species (*ibid.*). On the basis of modern distribution patterns and pollen size-frequency characteristics, two additional birches may have been members of the late glacial flora near Allenberg Bog. One of these, *B. populifolia,* has small pollen (mode 27 μ in three acetolyzed preparations; *ibid.*). Davis (1958) suggests that it may have occurred in the New England A zone vegetation where it

likely occupied disturbed sites. *Betula papyrifera* is also expected because it now grows mainly in the boreal forest. However, the relatively large pollen of this species (mode 33 μ in one acetolyzed preparation; Leopold, 1956a) does not correspond to measurements of fossil grains at Allenberg Bog.

Reviewing briefly the nature of the zone A vegetation at Allenberg Bog as it is has been interpreted here, the lower third of the zone seems to record the development of a more or less open boreal woodland similar to that which today occurs in the subarctic of northern Quebec. This appears to have persisted throughout most of the zone because few meaningful changes occur in zone A above 14.5 m. The woodland was preceded by a transitional vegetation type in which spruce and pine greatly increased in abundance. These changes may have been in response to a warming trend in the climate, as zone A overlies an interval of tundra-like vegetation apparently dominated by herbaceous communities with spruce probably infrequent in the entire region. Without information on the duration of the tundra, however, a simple successional change may be represented instead. The density of *Picea* and *Pinus* in various parts of zone A must remain conjectural until additional surface samples prove that the pollen rain in an open woodland is different from that in a more closed forest. If the landscape contributing to the regional pollen rain was incompletely covered by stands of *Picea glauca* and *P. mariana*, the latter being more abundant at wetter sites, various nontree communities dominated by sedges, grasses, *Artemisia*, other Compositae, and additional herbs occupied the openings. *Alnus* and *Myrica* were probably present at the lake edge and in other nearby wet habitats. *Salix* was also part of the vegetation, but it is not known whether dwarf or shrub species are represented. *Pinus Banksiana* and/or *P. resinosa* probably grew at dry sandy sites in the vicinity, and both *Abies balsamea* and *Larix laricina* were members of the regional vegetation although it is not possible to tell in what proportion they occurred in the forest because their pollen is usually underrepresented. *Carpinus caroliniana* and/or *Ostrya virginiana, Fraxinus nigra*, and *Quercus* spp. occurred at some distance from the basin, perhaps within 100 mi, but this is difficult to document with certainty.

Houghton and Protection Bogs

The two sites that remain to be discussed are associated with the Valley Heads moraine. Both have relatively thin A zones in comparison to the long interval of spruce domination at Allenberg Bog. In neither of them is there clear indication of a zone with high NAP percentages. The lowest spectra in each contain from 15 to 24 percent herb and shrub pollen, but this is in association with high values for *Picea* (40 to 50 percent). The absence of zone T at both localities may be a sampling deficiency although the samplers were pushed as deeply as possible. Pollen is present in the basal clay at Protection Bog, but is absent from similar sediments at Houghton Bog.

Zone A pollen spectra from both Valley Heads bogs compare favorably with upper A zone spectra Allenbreg Bog. The vegetation that presumably produced these pollen assemblages has just been reviewed and little additional information can be added here. In common with the other sites in southwestern New York, *Carpinus-Ostrya, Fraxinus,* and *Quercus* pollen occur in the A zone of both profiles. Lesser amounts of *Carya, Corylus,* and *Ulmus* pollen are present also. Low relative numbers of *Tsuga* pollen first appear in zone A at the two bogs and also near the beginning of this zone at Allenberg Bog. It is probable that hemlock was an extraregional species at this time because the few grains present could have been wind carried to the site from a distant source. All of these are minor pollen types, however, and the zone is clearly dominated by spruce and pine. *Pinus Banksiana* and/or *P. resinosa* were present. Except for the pollen of temperate tree species, the assemblages match the modern pollen rain accumulating today in the open, boreal woodland of subarctic northern Quebec and at points to the south within the boreal forest itself.

A maximum in the *Abies* curve occurs near the end of zone A in all four profiles but is best developed at Protection Bog. At this locality, and perhaps at the others as well, the maximum may represent an actual increase in the number of balsam fir near the basins. Rapidly declining spruce percentages associated with the fir maximum imply an abrupt and perhaps catastrophic change in the vegetation. If balsam fir was growing suppressed in a spruce-dominated woodland, deterioration of the spruce overstory might have released fir seedlings and saplings in the understory. The period during which fir thrived must have been relatively short because its pollen drops out of the counts soon after the maximum is reached. At present, *Abies balsamea* persists under dense forest cover but nearly full sunlight is needed for best development (Fowells, 1965). This is in agreement with its known quick response to release. High fir percentages near the end of the spruce zone occur over a wide area in the Northeast, although the peak is sometimes just within the zone and other times at its end (Cox, 1959; Deevey, 1943; and others).

Deevey (1943) suggests that high fir values, which often occur with a spruce maximum at New England sites, may represent a change in the vegetation brought about by the last major glacial advance. As such it would correlate with subzone A-4 discussed previously. Since the Protection Bog fir peak occurs in sediments accumulated about 10,500 B.P. (extrapolating from the two higher dates at this site assuming a constant sedimentation rate), considerably after the last or Valders glaciation, it seems best to view the peak as a successional event.

The radiocarbon dated Valley Heads profiles enable time stratigraphic correlations to be made between these sites and others in eastern North America. In New York State, few published pollen spectra are comparable in age to the late glacial A zone assemblage at Houghton Bog dated at 11,880 ± 730 B.P. (I-3290). Pollen spectra above and below sediments dated at 12,850 ± 250 B.P. from a bog in eastern New York (Connally & Sirkin, 1970) contain less spruce and more pine and birch pollen than equivalent spectra at sites in southwestern New York. At the King Ferry site in the Finger Lakes region of central New York (Cox, 1959; Brown *in* Deevey *et al.,* 1959) spruce wood, 11,410 ± 410 years old (Y-460), associated with a mastodon skeleton, was embedded in sediments dominated by spruce and pine pollen. Spruce accounts for over 80 percent of total AP; NAP, unfortunately, was not tallied. The microfossil flora was taken to record the presence of a boreal, coniferous forest in central New York (*ibid.*).

Spruce wood dated at 12,100 ± 400 B.P. (I-838; Buckley *et al.,* 1968) from along the Glacial Lake Iroquois strand in central Niagara County near Lockport, N.Y., is approximately the same age as the lower part of the Houghton Bog A zone. A pollen assemblage from silty clay associated with the organic bed from which the wood was taken (N. G. Miller, in prep.) is similar to Houghton Bog spectra of the same age. The main difference is the relative frequency of Cyperaceae pollen: 34 percent is found at the former site, while only 4 to 8 percent occurs at Houghton Bog. If all of the sedge pollen is considered to have been produced by the upland vegetation, it is likely that a considerably less dense spruce woodland occurred near Lockport than existed 50 mi south near Houghton Bog. If, on the other hand, habitats near the strand were especially favorable to aquatic, lowland members of the family, local overrepresentation could explain the difference. Seeds of *Eleocharis* cf. *palustris* are abundant in the organic bed and substantiate a case for a near-site origin of much of the " sedge " pollen. Species of *Eleocharis* probably grew in beach pools at the Lake Iroquois strand and along streams draining Lake Tonawanda which at this time occupied a portion of the lowland between the Niagara and Onondaga escarpments. Since pollen recovered from the lake sediments was carried there by both wind and moving water, near-site aquatic and semiaquatic species shedding pollen into the water would have an excellent chance of being strongly represented in the counts.

Cones of black spruce occur in the Lockport deposit and perhaps one other species of spruce is also represented. Spruce needles, seeds, and twigs are exceptionally abundant. Cone fragments and a single seed of *Larix laricina* establish the presence of this species. But apart from these fossils which indicate the presence of trees, a rich assemblage of mosses recovered from the organic bed permits recognition of several distinct, nonforest plant communities (N. G. Miller, in prep.). Rich fens must have been relatively common because both fen and fen edge mosses are abundant. Drier habitats, perhaps beach ridges, were present, and species which may have grown on or among the calcareous rocks of the nearby Niagara escarpment also occur. Only one species which today typically grows in shaded spruce forests was identified. Other species which sometimes grow in this habitat were found also, but these are less useful indicators because they occur at open sites as well. The absence of a dominant forest element in the moss flora probably means that the landscape along this part of the Iroquois strand was occupied by a patchwork of dry- and wet-site herb and moss communities and that spruce occurred some distance behind the beach. Most of the spruce macrofossils were probably carried to the site by drainage from the inland as is shown by their abraded nature. Nearly all the fossil mosses are characteristic boreal forest species. Most range northward to the arctic tundra, but many also occur in the Great Lakes states. The species of greatest phytogeographic interest are *Aulacomnium acuminatum* and *A. turgidum* whose present North American ranges center on the arctic and subarctic. The southernmost station for the former is along the north shore of Lake Superior, an area well-known for its relict, arctic-alpine plants. *Aulacomnium turgidum* has a greater number of occurrences along the southern edge of its range, but it also is widespread in the subarctic and arctic. In the East, disjunct stations are known from the high peak region in the Adirondack Mountains and from the White Mountains. These taxa indicate that arctic-alpine vascular plants

may also have grown near Lockport 12,000 years ago and raise the possibility that limited areas of tundra may have occurred in the region at this time.

Beyond New York State, but within glaciated eastern North America, spruce-rich forests were widely distributed 12,000 years ago. Their presence in southern New England (see Davis, 1965b) has already been mentioned. To the west in southern Ontario, the beginning of organic sedimentation and the upper part of zone A at Crieff Kettle Bog near Hamilton has been dated at 11,950 ± 350 B.P. (Karrow, 1963). Spruce pollen accounts for about 80 percent of total AP (Terasmae *in* Karrow, 1963), and the proportion of white to black spruce pollen is approximately six to one. *Abies, Betula, Pinus Banksiana,* and *Quercus* are the other main tree pollen types present. From 15 to 45 percent NAP occurs in the zone (based on sum AP), and *Ambrosia, Artemisia,* other Compositae, Cyperaceae, and Gramineae are the principal types identified. *Dryas* pollen occurs near the bottom of the zone.

The correspondence of the Houghton Bog date and the newly determined age of the Two Creeks forest bed (11,850 ± 100 B.P.; Broecker & Farrand, 1963) has been noted. West's reanalysis (1961) of the type Two Creeks locality in eastern Wisconsin produced spectra dominated in all levels except the bottom by up to 90 percent spruce pollen (based on AP + NAP sum). In the lowest spectrum, *Shepherdia canadensis* accounts for over 95 percent of total pollen. This heliophytic shrub may have been one of the first colonizers of surfaces freed for plant occupation in the area. One out of every six spruce grains was identified as *Picea mariana.* Spruce forest was also present farther westward in southeastern Minnesota at this time (the *Picea-Larix* Assemblage Zone of Cushing, 1967).

The spruce-dominated vegetation 12,000 years ago, however, was clearly not of uniform composition across the region from New England to Minnesota. The most obvious difference is the presence of high values for *Pinus* pollen in western New York and New England and their absence from sites in Michigan, Wisconsin, and Minnesota. Apparently, pines were a part of the late glacial A zone vegetation in the East, but did not occur in the contemporaneous vegetation of the Midwest. The available data (Wright, 1964; 1968b) indicate that the Appalachian region served as a full and late glacial refugium for the three main pine species, *P. Banksiana, P. resinosa,* and *P. Strobus,* which participated in the revegetation of the glaciated Northeast. The relative numbers of temperate deciduous tree pollen types also vary from site to site within the region. An accurate assessment of the variability in terms of climate, however, depends in part on a detailed knowledge of the pollen rain in existing boreal forest and woodland, the forest-tundra transition, and the tundra itself. This is not available at the present time. Also, it must be kept in mind that modern analogues for certain late glacial pollen assemblages may never be found because the vegetation which produced them may have been a mixture of species brought together by differing migration rates and may thus represent chance combinations of species which coexisted for varying periods of time following the withdrawal and disappearance of the ice.

South of the glacial boundary in Pennsylvania the vegetation 12,000 years ago was apparently much different from that found at this time in western New York. At Bear Meadows in central Pennsylvania (Kovar, 1964; Stingelin, 1965), pollen analysis of sediments below a radiocarbon date of 10,320 ± 290 B.P. (Westerfeld, 1961) produced spectra dominated by pine pollen (60 to 70 percent). Spruce is weakly represented (10 to 15 percent) and NAP totals about 10 percent of the sum. Similar spectra have been obtained by P. S. Martin from sediments below a C-14 date of 11,300 ± 1000 B.P. (Y-727; Guilday *et al.,* 1964) at the New Paris Sinkhole No. 4 in south-central Pennsylvania, 65 mi from Bear Meadows. The 3 m of cave filling beneath the dated horizon is dominated by *Pinus* pollen, which accounts for about 60 percent of the sum (AP + NAP). From 6 to 15 percent *Picea* pollen occurs across the same interval, and the rest of the sum from 20 to 30 percent, is comprised of Cichorioideae, other Compositae, Cyperaceae, and Gramineae pollen. Near-site and onsite plants likely produced much of the pollen in the nonarboreal category. The vegetation producing this assemblage may have resembled an open boreal woodland with spruce and jack(?) pine stands separated by open ground (*ibid.*). Above the dated level, *Pinus* remains dominant, but *Picea* drops to less than 5 percent of the sum, and Betulaceae, *Quercus,* and other temperate arboreal pollen taxa become strongly represented. This apparently records the movement of temperate forest elements into the area.

Sediments below the date contain bones of a large number of vertebrates whose modern ranges center southeast and west of Hudson Bay in boreal Canada. Of particular interest are the remains of at least three Labrador collared lemmings, a species that today occurs mainly within the tundra of northern Quebec. Also found were the bones of the 13-lined ground

squirrel and the sharp-tailed grouse, two prairie species whose occurrence substantiates the contention (Schmidt, 1938; see also Benninghoff, 1963) that an eastward extension of prairie elements occurred in late rather than postglacial time.

If the vegetation in central and southern Pennsylvania indeed was an open, boreal woodland like that existing beyond the north edge of the boreal forest today, an interpretation which is in part substantiated by the fossil vertebrates, the presence of a more closed spruce-pine forest to the north on glaciated terrain is difficult to understand because this zonation is the reverse of the current arrangement of these vegetation types in North America. Existing data are too sparse to establish the presence of the boreal forest in the region south of Pennsylvania and a taiga-tundra in a wide band between the ice margin and the forest during full glacial times, 18,000 years ago (cf. Martin, 1958a). If such a zonation existed, however, low relative numbers of spruce pollen in Pennsylvania about 11,500 years ago might have been produced by stragglers of the spruce migration that characterized this phase of revegetation of the glaciated region to the north. The apparent abundance of pine in Pennsylvania at this time, as shown by the work of Martin (Guilday *et al.*, 1964; Kovar, 1964), indicates that certain species of this genus may have dominated the landscape northward toward New York State. A floristic boundary separating spruce- and pine-rich forests must have existed somewhere between the two areas. If pines indeed were dominant behind the spruce forest during A zone time, this would help explain the rapid development of the B or pine zone following the disappearance of spruce from the region. In western New York, *Pinus Strobus* was the principal B zone pine. How early it was present in central Pennsylvania during late glacial time is not known.

The end of the A zone at both Houghton and Protection bogs can be dated by extrapolation. At the former locality, assuming that the pine peak occurred at the same time as it did at nearby Protection Bog and that the sedimentation rate was constant, the midpoint of the *Picea* decline is about 9500 B.P. Since the basal marl at Houghton Bog may have accumulated at a more rapid rate than the silty gyttja at Protection Bog, this date may be somewhat too young. The same type of calculation applied to data from Protection Bog yields an age of 10,500 B.P. for the same point in the spruce decline. Both age determinations are in accord with those listed by Ogden (1967b) who has concluded that the approximate synchroneity of the extinction of spruce forest across midlatitude eastern North America points toward a sudden climatic change at this time.

ZONE B

As the spruce-dominated A zone vegetation near the two Valley Heads sites disappeared 10,500 to 9500 years ago, the pollen record indicates that pines became increasingly abundant in the region. At Houghton, Protection, and Allenberg bogs the transition was abrupt. In contrast, spruce percentages at the Genesee Valley Peat Works gradually decline, although *Pinus* values increase rapidly. This is achieved mainly at the expense of various nonarboreal pollen types. High *Pinus* values are maintained upward well into spectra which seem equivalent to those in zone C-1 at the three other sites. Although *Pinus* drops to about 7 percent of the sum in the Genesee Valley profile above a depth of 1 m, that portion of the diagram in which percentages of both *Pinus* and *Tsuga* are high may be strongly influenced by onsite pine trees. *Pinus Strobus* pollen was the main type identified from this interval and the occurrence of white pine cones at various levels in the peat implies that white pine was growing locally. For this reason, the end of zone B was placed at 2.25 m near the midpoint of the *Tsuga* increase, even though above this level, *Pinus* percentages are still high. The A to B zone transition has not been dated at either Allenberg Bog or the Genesee Valley Peat Works, but, considering the proximity of all four sites, the disappearance of spruce may have been synchronous across the entire region.

The interval over which maximum zone B pine percentages occur in sediments at Protection Bog was dated at 9030 ± 150 B.P. (I-3551). This compares well with a date of 9310 ± 150 B.P. from an equivalent stratigraphic position at Crystal Lake in northwestern Pennsylvania (Walker & Hartman, 1960) where the entire postglacial pollen sequence parallels that in my profiles from western New York. The dated sample at Crystal Lake was taken from the level at which maximum *Pinus* values occur, although at this depth *Picea* still amounts to 10 percent of the sum. In southern New England, maximum relative and absolute numbers of pine pollen have been found in sediments about 9000 years old (Davis, 1967b; see also Davis, 1965b).

The ecological meaning of zone B has been discussed at length by Dansereau (1953) who presents a number of hypotheses to explain the widespread occurrence of maximum pine values following the disappearance of

the A zone spruce forests. A part of the difficulty in interpreting zone B lies in the well-known overrepresentation of pine pollen in sediments. With this in mind, Davis (1963, 1965b) has applied correction factors derived from a comparison of surface pollen accumulation and vegetation composition to a profile from northern Vermont. Her data indicate that maximum B zone pine percentages are an artifact caused by the low pollen productivity of the rest of the B zone vegetation. Pine trees were thought to have been rare in the region surrounding the basin in spite of the high relative pine pollen frequencies. This interpretation was later revised, however, when absolute pollen frequency data from Rogers Lake in southern Connecticut became available (Davis, 1967b). The deposition rate of oak, pine, and other arboreal pollen types was found to actually increase in zone B, and at certain levels the rate for pine was 18 times greater than later in postglacial time, implying that pines were truly abundant in the region during zone B time. Absolute pollen frequency determinations from Allenberg and Houghton bogs corroborate these findings, assuming that the sedimentation rate was uniform across zone **B** at these sites.

Either *Pinus Banksiana* or *P. resinosa* or both appear to have been members of the regional vegetation that contributed pollen to zone A sediments in western New York. Fairly high values for these species, members of *Pinus* subg. Pinus, persist through the lower part of zone B at all sites, but by the end of zone B time, only 1 to 3 percent occurs. Similar values are found in early postsettlement spectra before extensive plantings of pines belonging to subg. Pinus were made in the area. At this time, presumably, only *P. resinosa* was contributing subg. Pinus type pollen to the sediments. Today in western New York, native red pine is restricted to stations along the Genesee River (Zenkert, 1934).

Utilizing data provided by Whitehead (1964), a shift of the mode to a larger size class (figure 11), may indicate that *Pinus resinosa* was the principal B zone pine of subg. Pinus, while both *P. Banksiana* and *P. resinosa* may have been members of the zone A vegetation. However, the closeness in pollen size of these two species, as Whitehead emphasizes, makes positive identification impossible. Pines of subg. Pinus were infrequent in the regional vegetation at the west end of New York State after about 9000 B.P., while they appear to have been more abundant throughout the state before this date (see Cox, 1959). Prior to 10,500 B.P., red or jack pine or both were absent from Minnesota, but about this time they arrived at the southeast corner of the state, having migrated, probably north of the Great Lakes, from their refugium in the Appalachian Highlands of eastern North America (Wright, 1968b; Yeatman, 1967). Jack pine does not seem to have persisted south or west of the upper Great Lakes.

The relatively few *Pinus Strobus* grains which occur in the lower half of zone A imply that white pine was initially not near any of the basins. However, higher in zone A sediments, *P. Strobus* percentages increase indicating that white pine became more abundant regionally. This is most clearly seen in the Allenberg Bog section C diagram. It is certain, however, that white pine was present near Protection Bog during the A to B zone transition because a white pine cone was recovered from silty-clay gyttja at a depth of 5.75 m. Extrapolating from the two higher radiocarbon dates at this site, assuming a constant sedimentation rate, the cone was deposited approximately 10,000 years ago. At 5.75 m, pine pollen accounts for 35 percent of the sum. *Pinus* subg. Strobus and subg. Pinus types each amount to 6 percent; the remainder could not be identified to subgenus. Higher in zone B, a maximum of 25 percent *P. Strobus* pollen is reached and the dominant species of pine throughout B zone time at Protection Bog was clearly white pine. At other sites in southwestern New York, white pine also appears to have been one of the principal species which replaced spruce.

Pinus Strobus arrived in eastern Minnesota 7000 years ago from the east (Wright, 1968b). Its further migration was limited by eastward expansion of the prairie and oak savanna which began 8000 years ago in the upper Midwest. About 4000 years ago, prairie expansion ceased, and white pine began again to migrate westward reaching the northwest part of Minnesota about 2700 B.P., the western edge of its present distribution in North America. White pine in western New York 10,000 years ago supports Wright's contention that the species survived full glacial conditions in eastern North America.

Studies in the Allegheny National Forest of northwestern Pennsylvania (Hough & Forbes, 1943) indicate that *Pinus Strobus* may have played a successional role in the change from spruce to pine forest. Even-aged pine stands whose origin, in many cases, has been traced to an event that opened a part of the forest to seeding from nearby mature individuals occur in this region today. Understory white pines are absent because its seedlings do not survive in the shade. It is easy to visualize white pine seeding into openings created in

the deteriorating spruce forest 10,500 years ago. We know that mature, seed-producing white pines were established at this time near Protection Bog and probably elsewhere in the region. They seem to have coexisted temporarily with spruce whose actual abundance in the total vegetation at this time is not precisely known. Size-frequency measurements indicate that *Picea mariana* was the main spruce near Allenberg Bog at the end of zone A. Because this is principally a lowland, wet-site species, upland forests containing *Picea glauca,* which according to pollen size data was present earlier in zone A, may have been replaced by other communities. Considering the narrow stratigraphic interval across which spruce drops from high to low values, spruce forests must have rapidly disappeared, freeing more and more surfaces for occupation by pine and other B zone species. Wright (1964) suggests that spruce regeneration at this time was limited by summer temperatures which exceeded the tolerance of the species.

Extrapolating from the Protection Bog age determinations, the total duration of zone B in western New York seems to have been between 1500 and 2000 years. This is equivalent to about four white pine lifetimes, if we accept 450 years as the normal life span of the species (see Fowells, 1965). The occupation of a given site by successive generations of white pine may mean that other species (e.g., *Tsuga canadensis*) that normally would replace it in the region today had not yet migrated to the area. Since hemlock pollen does not occur in large numbers until some time after the B zone peak at 9030 ± 150 B.P., this hypothesis seems supported by my data. There was at least a four millenium lag in the migration of hemlock northward from somewhere in the unglaciated Appalachians following ice withdrawal from the Valley Heads moraine 13,000 years ago or earlier. In part, this was probably climatically controlled, but differential migration rates of species back onto glaciated terrain may explain the basic pattern of early postglacial pollen succession in western New York State.

In some of my profiles, zone B can be divided into a lower pine-birch subzone and an upper pine-oak subzone. A birch peak in the lower part of the zone is best developed at Allenberg Bog where it is associated with highs in the curves of *Carpinus-Ostrya, Fraxinus nigra,* and *Populus.* These features are less apparent at the other sites, although at Houghton Bog high percentages of *Betula* and *Carpinus-Ostrya* occur in the equivalent stratigraphic interval. Whether these changes have regional significance is doubtful, however, because they are less clearly defined at nearby Protection Bog where no peak is discernable in the *Betula* curve. *Ulmus* is well represented at most sites, suggesting that elms were an important part of the regional vegetation. In fact, the magnitude of elm percentages in zone B is only slightly less than that present in later postglacial time.

The presence of high birch values is not unique to western New York. Similar findings from southern New England have been reported by Davis (1958) and by Whitehead and Bentley (1963). These authors refer to the interval as subzone B-1. Since the peak occurs across the A/B zone boundary, birches may have been locally important members of the vegetation that existed during the transition from spruce to pine domination. In western New York, *Carpinus caroliniana* and/or *Ostrya virginiana, Fraxinus nigra,* and *Populus* spp. appear to have been present during this interval as well. Davis (1967a) mentions that the New England B-1 pollen assemblages compare well with modern surface samples from northern Minnesota and from the Lake Timagami region of Ontario. These localities are in the mixed coniferous-deciduous forest formation about 60 mi south of the boreal forest and may indicate that the climate of southern New England during B-1 time was cooler and drier than it is at present. Slightly lower *Betula* percentages and higher *Quercus* and *Ulmus* values characterize western New York State sites, but, otherwise, B-1 assemblages from this region agree with those from New England.

At Allenberg Bog where size measurements are available for zone B birch pollen, the configuration of the size-frequency curve shows that two species may have been present (figure 9). However, these cannot be identified with size data currently available from herbarium speciments of eastern North American birch species. Possibly *Betula populifolia, B. pumila,* or both were present, as these species have pollen intermediate in size between the small grains of the shrub birch, *B. glandulosa,* and the larger pollen of the tree species, *B. lenta* and *B. alleghaniensis.* If *B. populifolia* and *B. pumila* produced the mode at 25 μ, then the larger modal class near 27 μ may indicate the presence of one of the tree birches during the deposition of zone B. In zone C-1, the mode also occurs at 27 μ, but higher in the section it shifts to 26 μ. Although apparently only *B. lenta* and *B. alleghaniensis* produced the mode at 26 μ in upper C zone spectra, the meaning of the modes at 25 and 27 μ in zone B is obscure.

The upper portion of zone B in western New York is dominated by *Pinus Strobus* and *Quercus* pollen. In some of the profiles, *Betula, Carpinus-Ostrya, Fraxinus,* and *Populus* values are lower than they were near the

bottom of zone B. *Acer saccharum* was likely established in the region by the end of zone B. Arrival of oaks and expansion of the area occupied by them at locations near the basins is indicated by rapidly increasing relative numbers of oak pollen, although before this time some oaks were probably growing within 50 to 100 mi of the basins. The species involved are unknown, and either macrofossil evidence or improved pollen identification techniques are needed for specific determinations. However, *Quercus rubra* is one good candidate because of its current " northern " distribution and pioneer status, but other species could have been present also.

The entire B zone seems to record development of a white pine-oak forest. However, it is likely that the vegetation was quite complex at this time. Because of its broad ecological tolerances, white pine probably occurred in lowland valleys with elm and black ash and, in the upland, with oaks and/or sugar maple. The former community may have been similar to the White pine-American elm swamp forest that originally occupied the axes of some of the major valleys in Cattaraugus County (Gordon, 1940). Forest types containing white pine and oak species are also known from western New York at the present time. White pine and red, black, and white oak originally occupied dry sites on about 2 percent of Monroe County (Shanks, 1966), and similar stands undoubtedly occurred elsewhere in the Erie-Ontario Lowland. *Castanea dentata* and, at certain places, *Pinus rigida* were additional important members of this community. The pollen rain of this forest type has not been determined, and, considering the present distribution of vegetation in the lowland, it seems unlikely that a sample which was not influenced by pollen output from the surrounding mesophytic forests could be obtained for comparative purposes. In any case, neither *Castanea* nor *Pinus rigida* appear to have been members of the B zone vegetation according to pollen data currently available. Forests containing white pine and oak species are also known from well-drained sites, usually S-facing slopes, on the Allegheny Plateau.

The pine-oak subzone pollen assemblages seem to have no exact modern analogue, but Davis (1967a) points out they are closest to the modern pollen rain in southern Ontario near the boundary between the deciduous and coniferous-deciduous forest (see King & Kapp, 1963, sample 4). However, an important difference is the higher pine and oak percentages found in upper B zone spectra from southwestern New York State. Although the suggestion that an analogue of the pine-oak subzone is not in existence today seems premature, it is possible that a unique assemblage of species brought together by differential migration rates was present in western New York 9000 years ago.

ZONE C–1

Post-zone B sediments contain a record of the development and persistence of forests which contain the same species that now dominate existing forest types in western New York. Hemlock is an important tree in this region today and its pollen record is especially interesting and significant. The C-1 is set apart from the zones above it by high relative numbers of hemlock pollen and gradually increasing beech values. These features are retained when the relative frequency data from Houghton and Allenberg bogs are replotted on an absolute basis. *Tsuga* percentages increase markedly at the B/C-1 boundary and total *Pinus* values, with *P. Strobus* pollen predominating, reciprocally decline. Across a 30 cm interval at Protection Bog, *Tsuga* increases from 2 to 25 percent. Assuming that it took 26 years to deposit 1 cm of gyttja in the basin (the sedimentation rate between the two radiocarbon dates immediately higher in the section), about 800 years was needed to accumulate this thickness of sediment.

The abrupt nature of the increase and the weak expression of *Tsuga* in zone B suggests that the beginning of zone C-1 records initial invasion and expansion of hemlock in the region. At most of the sites, low relative numbers of hemlock pollen found in zones A and B probably represent grains blown in from distant sources. Unfortunately, detailed information on the dispersal of hemlock pollen is not available, but up to 7 percent has been found in surface sediments near Lansing, Michigan (Parmelee, 1947) at locations about 75 mi south of the limit of more or less continuous hemlock distribution in the State as mapped by E. L. Little, Jr. (*in* Fowells, 1965). According to the R values which I have calculated using several estimates of forest composition, hemlock pollen is somewhat overrepresented in both surface and presettlement spectra. This may also have been true during earlier postglacial time indicating that hemlock trees were actually somewhat less abundant in the total vegetation than the pollen record implies.

The ultimate cause of replacement of white pine is speculative. Arrival of hemlock in the region during its migration northward onto glaciated terrain has already been mentioned as one possibility, but whether hemlock was migrating at its fullest potential during

the time preceding its arrival in western New York or whether its movement was held in check by climate or soil development is not known. The latter would seem not to have been too critical because hemlock seeds are able to germinate on a variety of substrata; e.g., moist, well-decomposed litter, rotted wood, mineral soil, and moss mats or soil and rocks (Hough, 1960). Once hemlock was present, however, white pine replacement can be viewed as a successional event. Although in existing forests both white pine and hemlock are often periodic in occurrence, studies in the Allegheny National Forest (Hough & Forbes, 1943) have shown that when both are found together, white pine will drop out of the association as time passes because its seedlings do not become established under a dense canopy, while those of hemlock can.

At the present time hemlock occurs from the southern Appalachians northward across the glacial boundary to northern Maine, New Brunswick, and Nova Scotia. Westward it extends to eastern Kentucky, central Ohio, and through southern Ontario and northern Michigan to northeastern Wisconsin (Little *in* Fowells, 1965). The pollen record for *Tsuga* is not identical across this region, however, and although the main difference is the absence of two hemlock maxima from certain areas, a feature which will be discussed more fully under the heading Zone C-2, another variable is the magnitude of hemlock representation in sediments deposited immediately following high B zone pine percentages. In glaciated eastern North America from northwestern Pennsylvania to northern Maine (see Cox, 1959; Davis, 1965b; Deevey, 1951; Krauss & Kent, 1944; Potzger & Otto, 1943; Terasmae *in* Karrow, 1963; Walker & Hartman, 1960), maximum hemlock values appear early in pollen profiles, and at several sites in the southern part of this region where radiocarbon dates are available, the appearance of hemlock can be estimated at between 9300 and 8500 B.P. (Davis, 1967b; Walker & Hartman, 1960). Hemlock first appears near Halifax, Nova Scotia about this time as well, although maximum values were not reached until about 7100 years ago (Livingstone, 1968). In general, at sites in eastern North America which fall within the present limits of the Hemlock-white pine-northern hardwood forest region (Nichols, 1935), *Tsuga* accounts for 25 to 35 per cent of the sum directly above zone B. However, in southern New England, south of the forest boundary but still within the total range of hemlock, maximum C-1 hemlock values reach only 10 percent (Davis, 1967b). To the west in the Hemlock-white pine northern hardwood forest region of Michigan and Wisconsin, *Tsuga* pollen is also weakly represented in the equivalent stratigraphic interval. Unfortunately few C-14 dated pollen profiles are available from either state, but hemlock would seem to have reached the Douglas Lake region of Michigan (Wilson & Potzger, 1942) early in the period of oak-hardwood domination which probably is temporally equivalent to zone C-1 in the East. About 5 percent or less is present until some point later in postglacial time when an increase to 20 percent took place. In central Michigan, hemlock is consistently a part of the pollen record above a C-14 date of 7982 ± 250 B.P., but it accounts for only 5 percent or less of the sum (Gilliam *et al.,* 1966). West's diagram (1961) from Seidel Lake in eastern Wisconsin similarly shows that *Tsuga* appeared fairly early during the period of oak domination that followed the *Pinus* maximum, but hemlock never exceeded about 3 percent of the total until much higher in the section. Increasing *Tsuga* percentages in later postglacial sediments from this lake (= C-3 in western New York?), parallels the same trend at sites in northern Michigan. This change can also be observed in profiles from many other sites in the region (Messenger, 1966; Potzger, 1946).

Hemlock appears to have entered Michigan from the east, north of Lake Erie, and not from the south across the Prairie Peninsula, which apparently acted as an effective barrier to migration of hemlock, beech, and perhaps other species from the central Appalachians (Benninghoff, 1963). For example, in the diagram from Silver Lake in western Ohio (Ogden, 1966), low relative numbers of hemlock pollen (<5 percent) first occur 9800 years ago, but at several points higher in the section it completely drops out of the counts. Whenever hemlock pollen is found, it comprises only 2 to 3 percent of the sum, indicating that *Tsuga* was never very abundant in western Ohio. During postglacial time in this region, hemlock likely occurred intermittently in small, isolated stands, perhaps on N-facing slopes or in other suitable edaphic situations. At the present time Silver Lake is about 50 mi west of the limit of continuous hemlock distribution in Ohio.

Although hemlock first appeared at about the same time in western New York, Michigan, and northern Wisconsin, the early postglacial period of hemlock dominance characteristic of my western New York profiles is absent from sites to the west. In western New York where this occurs between about 8500 and 4300 B.P., the vegetation appears to have been remarkably stable. The only significant changes occur in the *Fagus* and *Quercus* curves. The former shows a long-term increase, while the latter undergoes a corresponding de-

cline. However, during the same period, the prairie and oak savanna expanded eastward in Minnesota (Wright, 1968a). It has not yet been established whether Wisconsin and Michigan were affected by the drier and warmer climate that probably induced this vegetation change, but if they were this might explain the meager representation of hemlock pollen in sediments accumulated during zone C-1 time at sites in the northern part of these states. Hemlock is known to grow best in a humid, cool climate and to be sensitive to drought which, when excessive, will result in death of the trees. It also follows that western New York State, where hemlock pollen is abundantly represented between 8500 and 4300 years ago, was cooler and more moist than the Midwest. When Minnesota and perhaps surrounding areas were undergoing a " xerothermic " interval, western New York State it appears was not.

Too few pollen profiles are available from the Erie-Ontario Lowland in central and western New York to determine whether the vegetation during zone C-1 time was the same on both sides of the tension zone which now exists in the area, or whether beech-maple and oak forests dominated the lowland vegetation as they did immediately preceding settlement of the region. Prior to settlement, hemlock apparently was much less abundant in the lowland than in the upland. Because development of this difference should be apparent in the pollen record, weaker representation of hemlock pollen in the lowland than the upland during the C-1 might indicate that the tension zone was established fairly early in postglacial time. Little difference is apparent in C-1 *Tsuga* values between available profiles from lowland and upland sites, however. For example, at Bullhead Pond (Cox, 1959), a small lake in central New York, 20 mi south of Lake Ontario, *Tsuga* accounts for about 20 percent of the sum, although generally less than 10 percent is present at Kennedys Bog near Rochester (Yeager, 1969). Somewhat higher percentages of hemlock pollen occur at some of my upland sites, but the difference hardly seems significant. At Cicero Swamp (Cox, 1959) and Pennellville Hidden Lake (Durkee, 1960), about 40 mi further east and near the present edge of the lowland deciduous forest region, *Tsuga* reaches about 40 percent of the sum in zone C-1. In general, pollen diagrams from both the upland and the lowland are enough alike to indicate that only minor differences occurred across the entire region, but further data are needed to treat this problem more adequately.

Forest vegetation developing during zone C-1 time in southwestern New York was very similar to that present in the region just prior to colonial settlement. Upper C-1 spectra closely match pollen assemblages which accumulated in the region from 1000 to 2000 years ago. This means that the regional vegetation, and very likely the climate, during both periods were the same. *Tsuga* and *Fagus* did not arrive in western New York at the same time and communities containing hemlock must have been well-developed when beech entered the region and began to expand. The long-term increase in *Fagus* values, which take place mainly at the expense of *Quercus*, can be interpreted as a trend toward increased mesophytism in the total vegetation. The prominence of beech in postglacial sediments from western New York is scarcely surprising in view of the important position this species holds in the Allegheny National Forest where it ranks highest of all forest species in establishment capacity, survival, and competition. Beech is even less dependent on certain kinds of seedbeds, soil moisture, or light than hemlock (Hough & Forbes, 1943). During zone B time, oak forest types may have occurred at a variety of sites, although at present they are found mostly on S- and SW-facing slopes in southern Cattaraugus County and in limited areas to the north. The pollen record indicates that with the passage of time these forests shrank in size and were in part replaced by more mesophytic associations containing hemlock, beech, sugar maple, and other northern hardwoods.

Overall, the C-1 vegetation was probably a mixture of forest types as complex as now occurs in the region. Pollen from most of the important tree species which at present exist in the area are variously represented in the zone; those that are not, such as *Prunus serotina* and *Magnolia acuminata,* are mainly insect-pollinated and therefore are rarely found as fossils. Both *Tilia* and *Fraxinus americana* and/or *F. pennsylvanica* (4-colpate *Fraxinus* grains) first appear at the beginning of the C-1 and are as well represented in this zone as higher in the profiles. Likewise, pollen from *Platanus occidentalis* was first encountered at about this time in the two Valley Heads bogs; however, to the south at Allenberg Bog small percentages are present throughout zone B. High *Platanus* values are prominent in zone C-1 at Houghton Bog where the outwash plain surrounding the bog may have been an especially favorable habitat for this species. *Juglans cinerea* first occurs in low relative numbers in the upper part of zone A and a few grains were encountered in zone B sediments, but at all sites the postglacial maximum is reached

at some point within the C-1. *Ulmus* and *Betula* continue to hold prominent positions in the vegetation of the region. At Allenberg and Protection bogs, birch values are somewhat higher near the middle of the zone than at either beginning or end. Size-frequency measurements of birch pollen at the former location indicate that the tree birches, *B. lenta* and *B. alleghaniensis* were the main species present. Low relative numbers of *Castanea dentata* pollen first appear in zone C-1 at Allenberg and Houghton bogs, although this species regularly occurs from near the beginning of the C-2 upward at Protection Bog. Local habitat differences near the basins probably explain the disparity.

ZONE C–2

In southwestern New York zone C-2 is characterized by low hemlock percentages and increased values for broadleaf deciduous tree taxa. It is an interval between two successive hemlock maxima. The zone is represented in the Houghton, Protection, and Allenberg Bog profiles, but is absent from the Genesee Valley Peat Works diagram because the bulldozed uppermost sediments at this site were not sampled. In my profiles the lower zone boundary can be readily located at the midpoint of the abrupt hemlock decline which, at Protection Bog, has been dated at 4390 ± 110 B.P. (I–3550). However, placement of the upper boundary is arbitrary because of the absence of any clear stratigraphic markers. I have chosen a point where percentages of deciduous tree taxa are reduced over their C-2 maxima and where hemlock just begins to exceed 10 to 15 percent of the sum. Accepting this placement, zone C-2 ended 1270 ± 95 years ago (I–3549) at Protection Bog. This is from 500 to 800 years younger than other age determinations of the C–2/C-3 transition from eastern North America (see Davis, 1965b) but the difference may not be significant due to variability inherent in radiocarbon dates. Using the rate of sediment accumulation between the two highest C-14 dates at Protection Bog (0.069 cm/year), hemlock percentages decrease from 23 to 8 percent in about 350 years. This is only an estimation, however, because the sedimentation rate may have been less in the upper part of the gyttja than between the dated levels in the gyttja and peat. Furthermore, the 25 cm over which the reduction in hemlock percentages takes place reflects the sampling interval used in this part of the profile. Since the same change could have taken place in less than 25 cm the time interval may actually have been shorter. Pollen stratigraphy across the transition should be determined in detail in future studies.

In relative frequency diagrams, the *Tsuga* reduction is compensated for by increases in a number of other arboreal pollen types, principally *Fagus, Acer saccharum, Betula, Quercus,* and *Carya.* Lesser increases also occur in *Pinus Strobus, Fraxinus americana* and/or *F. pennsylvanica, F. nigra,* and at one site, *Carpinus-Ostrya.* In no case is any increase as prominent as the *Tsuga* decline. Size-frequency measurements from the upper and lower halves of zone C-2 at Allenberg Bog indicate that *Betula lenta* and/or *B. alleghaniensis* were the main birches contributing to the pollen rain, but possibly a third species was present during the deposition of the upper part of the zone.

These changes indicate modifications in the regional vegetation which simultaneously favored the expansion of dry site oak and hickory forests and mesic communities containing beech, sugar maple, and birch. Traditionally zone C-2 in eastern North America has been interpreted as a xerothermic interval, a period of warm and dry climate during which oak and hickory forests expanded at the expense of more mesophytic associations (see Deevey, 1949). Although a decrease in the representation of hemlock, a strongly mesophytic species, and the corresponding increase in oak and hickory in western New York State is the expected pattern, if the xerothermic interpretation is accepted, coordinated increases in *Acer saccharum, Betula lenta* and/or *B. alleghaniensis,* and *Fagus grandifolia,* all of which also are mesophytes, are contradictory.

A drier, more continental climate during the C-2 would be better documented if an analogue for the vegetation could be found where such a climate prevails at the present time. The Beech-maple forest region of central Ohio and Indiana is a logical place to look for surface pollen assemblages similar to C-2 spectra from southwestern New York, but unfortunately no systematic study of the recent or subrecent pollen rain in Ohio and Indiana has been made. Pollen profiles from this area provide some comparative data, however. The topmost spectra in diagrams from north-central and northeastern Ohio presented by Sears (1942), which in most cases probably represent the subrecent pollen rain, do not match any of my C-2 assemblages, nor do spectra from just beneath the post-settlement *Ambrosia* peak at Silver Lake in western Ohio (Ogden, 1966). In both areas, *Quercus* and *Carya* values are larger and *Fagus* representation is much weaker than at any of my southwestern New York

sites. However, the lack of correspondence is not conclusive proof of the absence of a relationship because the pollen rain has been determined at so few sites in this part of the Midwest. Until such information is forthcoming, it seems best to reserve judgment on the current existence of a probable analogue for the C-2 vegetation.

It has been postulated that a wedge of prairie vegetation extended through central Indiana and Ohio during the putative mid-postglacial xerothermic interval (see Benninghoff, 1963). This hypothesis was used by Shanks (1966) to explain the origin of prairie remnants in oak openings in the Erie-Ontario Lowland of western New York. There is, however, no C-2 increase in grass pollen at any of the sites studied in this area. All C-2 spectra are dominated by arboreal pollen and in only a few cases does nonarboreal pollen account for more than 3 percent of the sum. In these instances, NAP is clearly of local derivation. Of some interest in this regard, however, is the presence of *Ephedra* pollen in zone C-2 at Protection Bog. If it could be established that *Ephedra* species were growing in the region during zone C-2 time, the argument for an interval of xeric, continental climate would be improved. However, Maher's recent review (1964) has shown that *Ephedra* pollen, which has been found widely in the Great Lakes region, is not limited to any one stratigraphic interval, but rather its pollen occurs sporadically in both late and postglacial deposits. This fact and the presence of *Ephedra* pollen in surface samples near Lake Simcoe, north of Lake Ontario (King & Kapp, 1963) and elsewhere, implies that an extraregional origin, through long-distance wind transport from the southwestern United States, is the most likely explanation for the presence of *Ephedra* pollen in western New York. The occurrence of *Liquidambar* pollen in both late and postglacial sediments in this region can be explained in the same way. At present the northern limit of sweet gum is southern Ohio and central West Virginia about 300 mi south and southwest of the sites included in this study.

In eastern North America, pollen profiles with two hemlock maxima separated by a single interval of low hemlock percentages are known from a broad area including northwestern Pennsylvania (Walker & Hartman, 1960), New York State (Cox, 1959; McCulloch, 1939; Dunham, 1965; Durkee, 1960), northern Vermont (Davis, 1965b), southern Vermont (Whitehead & Bentley, 1963), southern New England (Davis, 1967b; Deevey, 1939, 1943), and Maine (Deevey, 1951). In Canada, a hemlock decline is present in what appears to be a top-truncated profile at a site west of Hamilton, Ontario (Terasmae *in* Karrow, 1963). A *Tsuga* minimum also occurs in profiles from north of Toronto (McAndrews, 1970), from the Gatineau Valley region of Quebec, 30 to 60 mi north of Ottawa (Potzger & Courtemanche, 1956), and farther east in Nova Scotia (Livingstone, 1968). South of the glacial boundary at Bear Meadows Bog in central Pennsylvania, (Kovar, 1964) a mid-postglacial *Tsuga* minimum also occurs. It remains to be established, however, whether the hemlock decline is strictly synchronous over the entire region just discussed. Radiocarbon dates are available from only scattered localities but they show a surprising degree of accordance. The Protection Bog date of 4390 ± 110 B.P. agrees favorably with the *Tsuga* minimum which started at Rogers Lake, Connecticut about 4100 years ago (Davis, 1967b) and with the abrupt *Tsuga* decline dated at 4540 ± 140 B.P. at Crystal Lake near Halifax, Nova Scotia (Livingstone, 1968).

Can the hemlock decline be explained in any other way than by postulating a xerothermic interval? Viewing the tripartite C zone as a unit, the decline seems to occur at a time when soil development had progressed to a point where, by late C-1 time, the soil supported the same forest types that exist in the area today. Furthermore, the pollen diagrams indicate that with the possible exception of *Castanea,* no new taxa entered the region following deposition of the lower third of zone C-1, although data are not available on the immigration of *Liriodendron tulipifera, Magnolia acuminata, Prunus serotina,* and a few others which, while not important species regionally, are nonetheless significant members of some forest communities. Whatever was responsible for modifications in the mid-postglacial vegetation of southwestern New York seems to have changed what had become a fairly stable situation, at least with respect to entry of new species into the area.

In any event, hemlock appears to be the key to the interpretation of zone C-2. The relative frequency diagrams clearly depict a reduction in *Tsuga* percentages and an enlargement of values for temperate deciduous tree pollen types. It is difficult, however, to determine which was cause and which effect because of the nature of expressing data in percentages; *i.e.*, when the relative numbers of one category increase, a concomitant reduction in one or several others must occur. Therefore, the hemlock decline could represent an actual reduction in the number of *Tusga* grains being deposited per year or an increase in the deposition rates of *Fagus, Acer saccharum, Quercus,* and other pollen types while deposition of *Tsuga* pollen remained constant. In the

former case, increases in relative numbers of deciduous tree taxa would be artifacts of the percentage system providing their deposition rates remained constant; in the latter, the converse would pertain.

Insofar as absolute pollen frequency or the number of grains/unit volume of sediment represents actual deposition rates of the various pollen types, the absolute frequency diagram from Houghton Bog shows that a significant reduction in the numbers of *Tsuga* pollen /ml took place across the C-1/C-2 boundary, and that low absolute numbers persist throughout zone C-2. Of interest also is the fact that *Fagus, Acer saccharum, Quercus,* and *Betula,* which show the greatest increase in relative frequency during the change from zone C-1 to zone C-2, are not any more strongly represented in the C-2 than in the upper part of the C-1. Although these features are meaningful only if the rate of sediment accumulation was constant across the interval (and unfortunately radiocarbon dates which would enable its determination at Houghton Bog are not available), at sites in eastern North America where sedimentation rates have been determined (Davis, 1967b; Ogden, 1967a), it was more or less constant between late C-1 and late C-2 time. This may not be universally true in all small lake basins, but, in the absence of differences in sediment lithology, it seems reasonable to extend the assumption of a uniform sedimentation rate to Houghton Bog.

The absolute pollen frequency data indicate that the C-2 modifications in the relative frequency diagrams were produced mainly by a decrease in the absolute numbers of hemlock, a species whose silvical characteristics are fairly well known (Fowells, 1965; Hough, 1960). Hemlock mortality can be caused by a variety of environmental factors, but drought is most important because of hemlock's shallow root system. Severe damage to hemlock stands over a broad area following the droughts of the early 1930's is well documented in the literature. For example, Secrest *et al.* (1941) estimate that 50 million board feet of hemlock died in the 230,000-acre Menominee Indian Reservation in Wisconsin during the 3 years between 1931 and 1933. These authorities demonstrated that under drought conditions root tips are rapidly killed and gradually larger roots become weakened leaving affected trees open to fungus and insect attack. To the east, hemlock mortality during the same drought period has been recorded at the Allegheny National Forest (Hough, 1936b) and near New Haven, Connecticut, where, in a 0.1 acre plot, dead hemlock saplings and trees comprised 75 percent of the total sample (Stickel, 1933). Near New Haven, hemlock seedlings were killed outright and mortality in all size classes probably was enhanced by shallow soils developed directly over bedrock.

Data from a more detailed study on the effect of the 1930 drought on different forest types in central Pennsylvania (McIntyre & Schnur, 1936) supplies additional pertinent information. Examination of 23 plots spread among chestnut oak, hemlock, scarlet oak-black oak, and white pine-chestnut oak forest types showed that 84 percent of the total basal area of hemlock was lost from the sample. By comparison, black oak lost 52 percent, chestnut oak 28 percent, red oak 26 percent, and sugar maple 11 percent. Before the drought, the four hemlock-type plots contained abundant *Tsuga canadensis*, 60, 67, 78, and 80 percent expressed as a percentage of total basal area, while, after the drought, the relative dominance of hemlock was reduced to 2, 6, 66, and 24 percent in the same plots. The hemlock-type changed from one dominated by this species to one of mixed composition, mainly chestnut and red oak with much smaller amounts of hemlock. In a general way, this change parallels that observed in zone C-2 sediments from western New York with the exception of the importance of beech, sugar maple, and yellow and/or sweet birch in C-2 sediments from this region.

I suggest, therefore, that the hemlock decline can be viewed as a response to several severe drought years. The recorded devastation of hemlock during the 1930 drought from Wisconsin to southern Connecticut, and the accordance of the dates of the hemlock decline between western New York, New England, and Nova Scotia furnish the basis for postulating that widespread droughts might also have occurred about 4400 years ago. This new hypothesis, which can be partly tested by obtaining additional radiocarbon dates, to further check the synchroneity of the mid-postglacial hemlock decline, differs from the xerothermic interpretation in the nature and duration of the warm-dry climatic optimum. I feel that the modifications in the pollen record can be as well explained by postulating a series of severe droughts, perhaps distributed over several centuries or even over much less time, as by postulating an interval of xeric, continental climate lasting several millenia.

The return of *Tsuga* to a position of prominence in the pollen diagrams by zone C-3 time may represent the orderly and gradual succession of hemlock back into communities where it was at one time present. Competition between hemlock and other mesophytes, particularly beech, would accompany this change and

would affect the speed of hemlock reestablishment. *Tsuga* was never completely eliminated from the region because its pollen was continuously being deposited, even though in one instance it dropped as low as 4 percent of the sum. *Tsuga* likely survived in especially favorable edaphic situations, perhaps in deep gullies that were cooler and more moist than the surrounding upland.

If the decline in hemlock alone produced the C-2 modifications in pollen diagrams from southwestern New York, biotic factors rather than climate must also be considered as possible causative agents. Certain insects, including two species of hemlock loopers and the hemlock borer, are known to cause local mortality, as are foraging deer, porcupines, and rabbits (Fowells, 1965). Man may also have played a role. The Protection Bog date for the C-1/C-2 boundary corresponds to a period during which central and western New York was occupied by Indians of the Lamoka culture (Ritchie, 1969). They subsisted by hunting, fishing, and gathering; agriculture came somewhat later, perhaps about 1000 B.C. Little is known about the hunting techniques of these Indians, but apparently they secured large game, mostly white-tailed deer, with javelins propelled by throwing boards. They probably used dogs during the hunt and it is not inconceivable that fire was used to drive game. Hemlock is known to be vulnerable to fire damage, and, although old trees may survive light surface fires because of their thick bark, the roots are easily damaged by a burn that extends deeper than loose surface litter.

I attempted to measure the influence and periodicity of past fires in southwestern New York by recording the number of charcoal fragments over 30 μ in size while counting to the basic pollen sum, but charcoal frequency does not seem to have been any greater in zone C-2 than in C-1. However, the counting technique needs refinement before fire damage can be ruled out completely. For one thing, charcoal is brittle and larger pieces probably fragment during maceration, indicating that a smaller minimum size should have been established before counting. Of more serious consequence is the 25 cm sampling interval which is too great to regularly document such catastrophic events as fires. While I cannot rule out direct or indirect biotic interaction as the cause of hemlock decline, it seems unlikely that a biological agent would have led to a reduction in hemlock percentages over the broad area in which they occur. Locally biological agents may have been important, but certainly not across many hundreds of miles.

In some regions of northeastern North America, two *Fagus* maxima occur in sediments which are approximately contemporaneous with those of zone C-2 in western New York. For example at Silver Lake in western Ohio, Ogden (1966) considers the xerothermic interval to be represented by a minimum in beech pollen covering the interval between 3600 and 1300 B.P. This is about the same time period during which a *Fagus* minimum has been found in southern New England deposits (Davis, 1967b; see also Deevey, 1943). The only diagram from New York State in which a similar change occurs is Cox's undated Consaulus Bog profile (1959) from eastern New York near Albany. In this profile, the *Fagus* and *Tsuga* minima are not coordinated as they are in southern New England, but rather the former occurs slightly above the latter. Although *Fagus* is characterized by erratic fluctuations in certain other of Cox's diagrams, it is strongly represented in zone C-2 in all of them. The significance of the bimodal *Fagus* curve in deposits to the east and west of southwestern New York is not known. Since *Fagus* and *Tsuga* minima are not entirely synchronous, it seems likely that different factors were responsible in each case. The relationship between the two should be pursued.

ZONE C–3

Two important changes in the pollen record characterize this zone, the most recent in origin. These are the return of *Tsuga* (subzone C-3a) and the occurrence of high percentages of NAP above the presettlement /postsettlement boundary (subzone C-3b). Following the C-2 *Tsuga* minimum, hemlock values steadily increase higher in the profiles until near the end of the C-3a, the lower of the two subzones, where they are of similar magnitude to those of zone C-1. Percentages of deciduous tree taxa are reduced over their C-2 maxima, but they still remain strongly represented upward to the C-3a/C-3b boundary. Across this interval at the three sites where zone C-3 sediments were sampled, *Tsuga* increases mainly at the expense of *Fagus,* indicating an increased role for the former in the regional vegetation. This may have been enhanced by a trend toward a moister and a somewhat cooler climate which many feel has prevailed during the past several millenia (Sears, 1932) and may represent a continuation of succession begun during zone C-2 time.

This climatic trend seems confirmed at sites in northern New York (Durkee, 1960) and Canada (Potzger & Courtemanche, 1956) by a *Picea* increase in sedi-

ments that appear equivalent to zone C-3 sediments in western New York. Spruce, although sparsely represented in the upper 25 cm in Houghton and Protection Bogs, shows a distinct increase upward in zone C-3 at Allenberg Bog. Spruce pollen in this zone at the two Valley Heads bogs is mostly restricted to postsettlement spectra and, therefore, probably originated mainly from planted trees. At Allenberg Bog, however, spruce occurs regularly throughout zones C-2 and C-3 but apparently was absent near the sampling point during the deposition of zone C-1. The small size of spruce pollen (generally $<92\ \mu$) in both the C-2 and C-3 indicates the presence of only *Picea mariana* which likely grew on the bog mat. Two grains larger than 100 μ found in zone C-3b at Allenberg Bog probably were contributed by introduced cultivated species. The Allenberg Bog spruce increase needs further documentation in western New York because, rather than indicating a climatic trend, changes in the hydrology of the peat deposit, induced by either physiographic modifications or biotic factors (e.g., beavers), may explain what at the present time appears to be only a localized increase.

In New England, *Castanea* pollen shows a decided increase in the C-3 (Davis, 1969; Deevey, 1939), but this is not true in southwestern New York. Although regularly present upward from either zones C-1 or C-2 in the deposits I have studied, maximum *Castanea* values are reached near the end of the C-2 at Houghton Bog (1.8 percent) and near the middle of this zone at Allenberg Bog (4.2 percent). Less than 1 percent occurs at equivalent positions in the Protection Bog profile. *Castanea* was recorded in the original lot survey data only around Allenberg Bog, and, according to Gordon (1940), presettlement distribution of chestnut mainly included the southern part of Cattaraugus County where it grew with oak on dry upper plateau slopes and tops and in mixed mesophytic forests. Since Allenberg Bog is near the area of maximum chestnut occurrence while the two Valley Heads sites are about 25 mi to the north, my profiles, taken at face value, indicate that chestnut was never very abundant north of central Cattaraugus County in the Allegheny Plateau region of western New York.

Increasing *Tsuga* percentages in sediments that appear stratigraphically equivalent to the C-3a in western New York occur across an area that approximately coincides with the Hemlock-white pine-northern hardwood forest region. A clearly defined hemlock increase is not apparent in profiles from Nova Scotia, however. As was the case in zone C-1, maximum values attained by *Tsuga* vary from district to district. For example, hemlock does not exceed 10 percent in the C-3 just south of the forest region at Rogers Lake, Connecticut, while in western New York it reaches over 25 percent. At Rogers Lake, the highest C-3 hemlock percentages occur between about 1500 B.P. and the *Ambrosia* peak, which marks the advent of European settlement.

To the west but still within the forest region, the hemlock increase is more pronounced and parallels my findings in western New York. The C-14-dated Maple River Township Bog diagram prepared by Hushen and Benninghoff (unpublished ms.) from Emmet County near the northern tip of the Lower Peninsula of Michigan shows hemlock weakly represented (10 percent or less of the sum) between 4000 and about 3200 B.P., at which time an increase began. After several erratic fluctuations upward in the profile, hemlock accounts for 50 percent of the sum in two spectra just beneath the presettlement/postsettlement boundary. This change is accomplished largely at the expense of *Pinus*. Hemlock is weakly represented during C-1 and C-2 time in profiles from Michigan and Wisconsin, but a few *Tsuga* stands probably existed at favorable sites in these states. The *Tsuga* increase can be viewed as an expansion of these colonies, or, alternately, immigration from some source area may be represented. In all, the pollen record for hemlock is worthy of continued study. As more C-14-dated profiles become available from southern Ontario, which appears to have been the principal westward migration route for hemlock, a more critical analysis of its postglacial history will be possible.

The settlement of western New York, which began about 1800, and the attendant forest clearance is sharply marked by increasing NAP percentages and by the presence of wind-blown silt and clay in the Allenberg, Houghton, and Protection Bog profiles. Arboreal pollen drops to 50 percent or less of the sum over a very narrow interval indicating the castastrophic effect of European settlement on the natural vegetation. Although there is no clear evidence of Indian agriculture in any of my diagrams, low but perhaps significant percentages of *Ambrosia* and *Rumex* pollen which expand upward from zone C-3a below the presettlement/postsettlement boundary, may have originated from weeds occupying cleared areas where corn, squash, and beans were being grown by the Indians. It might be claimed that pollen of these types originated from more recent sediments, but *Plantago* pollen, which would be expected to show the same behavior in the pollen diagrams, does not occur below the boundary except for occasional, single grain occurrences. Rayback's map (1966) of known Indian

settlements shows a concentration of villages just west of Allenberg Bog in eastern Chautauqua and western Cattaraugus Counties. Other villages are known from near the head of Cattaraugus Creek fairly close to both Houghton and Protection Bogs. I do not know how many of these sites were inhabited by agricultural Indians or exactly at what times they were occupied, but the high incidence of Indian habitation in certain parts of southwestern New York indicates that any associated agricultural activities could be recorded in zone C-3 sediments.

Pollen from cultivated species is found from the beginning of subzone C-3b to the surface. Agriculture indicators, including *Zea* and pollen from other cereals (counted as Gramineae), occur at Protection, Houghton, and Allenberg Bogs, while *Fagopyrum,* buckwheat, is found only at the two last named sites. *Ambrosia* pollen is the dominant NAP type in the subzone and reflects the high incidence of disturbed, nonforest habitats where the common *A. artemisiifolia* and *A. trifida,* and the less frequent adventive, *A. psilostachya,* continue to flourish today. Maximum *Plantago, Rumex,* Cheno-Am, and Cichorioideae values are further evidence of the abundance of surfaces occupied by weedy species. Peak high-spine Compositae percentages may be in part due to increased frequencies of weedy species, but they could also reflect a local change in bog surface conditions favoring an increase in onsite taxa such as certain species of *Bidens.*

Summary and Conclusions

1. All of western New York except the Salamanca re-entrant, a semicircular area approximately bounded by the present course of the Allegheny River, was apparently ice-covered sometime during the Wisconsin glaciation. The various drift sheets in the region lack definitive dates, but the following correlations have been used in a recent review of the Pleistocene geology of New York State (Muller, 1965):

   Lake Escarpment-Valley Heads moraine: assigned to the Port Huron (Mankato) Substage, ca. 13,000 B.P.;
   Kent (Binghamton) moraine: assigned to Cary Substage, minimum date 14,000 B.P.;
   Olean moraine: pre-Cary (may be Tazewell or earlier).

   Other moraines associated with these are considered short recessional still-stands or minor readvances of the ice margin. Recently obtained C-14 age determinations, which indicate the Kent ice overrode the area around Cleveland, Ohio, about 23,250 years ago (White, 1968), and studies by Calkin (1970) will necessitate some revision in the above chronology. Recession to a point north of the Niagara escarpment in northwestern New York State was complete by 12,500 B.P. and ice apparently never again readvanced into western New York.
2. Pollen succession was studied in sediments from four basins located on drift sheets of different age; viz., Houghton and Protection Bogs associated with the Valley Heads moraine, Allenberg Bog on Kent drift, and the Genesee Valley Peat Works on Olean drift. Houghton and Protection Bogs are 10 mi apart, and Allenberg Bog is about 30 mi southwest of these. The Peat Works is 35 mi southeast of the former two sites and 50 mi east of Allenberg Bog.
3. The Portage escarpment separates western New York into two physiographic divisions: the Allegheny Plateau in the south and the Erie-Onatrio Lowland in the north. At the time of arrival of European settlers, the entire region was forested except for limited areas of prairie-like openings in the lowland. Forests of the Hemlock-white pine-northern hardwood Formation covered the upland, while beech-sugar maple and oak-hickory communities belonging to the Deciduous forest Formation occurred in the lowland. The ecotone between the two was not sharp and large inclusions of hemlock-hardwoods have been identified in the lowland. Upland oak forests are mainly limited to dry plateau tops and S-facing slopes near the Pennsylvania border.
4. An analysis of the bearing-trees recorded in the original lot survey notes for areas around Houghton, Protection, and Allenberg Bogs shows *Fagus grandifolia,* followed by *Acer saccharum,* to have the largest importance values. *Tsuga canadensis* is third in importance in two of the three areas. When frequency of mention data were computed from the same survey notes, *Fagus* continues to head the list. Second and third in frequency are *Acer saccharum* and *Tsuga canadensis* around Allenberg Bog, *Acer saccharum* and *Tilia americana* about Houghton Bog, and *Tsuga canadensis* and *Acer saccharum* around Protection Bog. Point-quarter sampling of three existing forest stands shows dominance by the same three leading species but with a change in the order of decreasing importance values. At all three sites, *Acer saccharum* heads the list followed by *Fagus grandifolia* and *Tsuga canadensis.*
5. The relative frequency of different pollen types in surface and presettlement spectra, divided by a percentage estimate of the importance of species in a vegetation sample contributing a given pollen type, provides a measure of the degree of representation of these pollen types in relation to the vegetation surrounding a depositional basin. These ratios or R values were calculated in several ways using surface pollen spectra compared with composition data collected by the U.S. Forest Service in existing forests and presettlement spectra compared with importance percentages and frequency of mention values derived from the original lot survey data. The computations indicate that in recent and subrecent sediment samples from western New York, pollen from *Betula* spp., *Pinus* spp., *Quercus* spp., *Tsuga canadensis,* and *Ulmus* spp. are overrepre-

sented, *Carpinus caroliniana* and/or *Ostrya virginiana, Fagus grandifolia,* and *Juglans cinerea* are proportionately represented, and that *Acer rubrum, A. saccharum, Castanea dentata, Carya* spp., *Fraxinus americana* and/or *F. pennsylvanica, F. nigra, Populus* spp., and *Tilia americana* are underrepresented.

6. A clearly defined T zone characterized by 50 percent or more nonarboreal pollen underlying a zone of spruce pollen domination was found in basal inorganic sediments only at Allenberg Bog. T zone pollen assemblages contain 20 percent *Picea,* 10 percent *Pinus,* 3 to 8 percent *Quercus,* 3 to 5 percent *Fraxinus nigra,* 15 to 25 percent Cyperaceae, about 10 percent Gramineae, and numerous other NAP types, and closely match the pollen rain today in the boreal forest-tundra ecotone at Fort Churchill, Manitoba where discontinuous spruce stands occur interspersed with herbaceous communities in a park-tundra. This implies that the climate in southwestern New York during the deposition of zone T was probably similar to that in this part of the subarctic today. No positive tundra indicator pollen types were found, although microspores of a subarctic and boreal species, *Selaginella selaginoides*, occur in several spectra.
7. Abundant herb pollen was present in basal sediments at the Genesee Valley Peat Works, but a zone in which spruce dominates is not present higher in the profile, making the meaning of the basal herb-spruce-pine assemblage at this site somewhat obscure. If local overrepresentation and redeposition were not operative, then an open vegetation perhaps similar to the park-tundra of T zone time at Allenberg Bog existed around the Genesee Valley site. However, there is some evidence that the pollen rain was influenced by near- and onsite herbs and, therefore, that the regional vegetation was a denser spruce-pine forest. Since the peat works are on the oldest drift sheet in western New York, the basal sediments may antedate comparable deposits elsewhere in eastern North America. If subsequent C-14 dating bears out their antiquity and if the pollen assemblage is taken at face value, a park-tundra may have covered the Allegheny Plateau in southern New York during the " classical " Wisconsin glaciations. More data are needed from additional sites in the region to further document this hypothesis.
8. Zone A at Allenberg Bog shows a long interval of domination by spruce and pine pollen. Changes in *Fraxinus nigra, Quercus, Pinus,* and *Picea* percentages permit subdivision of the zone following the sequence recognized in certain profiles from southern New England where such changes have been interpreted as vegetation modifications in response to the Two Creeks-Valders climatic changes. However, absolute pollen frequency data from Allenberg Bog indicate that an increase in the absolute numbers of spruce and pine pollen being deposited per unit volume of sediment — evidence of an increased abundance of spruce-pine forests on the landscape — was responsible for changes in the *Quercus* and *Fraxinus nigra* curves at this site. Absolute numbers of these pollen types remained more or less constant across the interval.
9. Zone A pollen assemblages from Allenberg, Houghton, and Protection Bogs contain both *Picea glauca* and *P. mariana* and are similar to existing surface pollen accumulations in the open boreal woodland of central Quebec. In contrast to the situation in Michigan, Wisconsin, and Minnesota, *Pinus Banksiana* and/or *P. resinosa* grew in southwestern New York during zone A time. *Abies balsamea* and *Larix laricina* were members of the A zone forests, and deciduous trees, whose pollen consistently occurs in the zone, may have occupied favorable sites within some tens of miles from the basins. This is particularly true of *Quercus* spp. and *Fraxinus nigra*, and perhaps *Carpinus caroliniana* and/or *Ostrya virginiana* also. The presence of *Acer, Carya, Juglans, Tsuga,* and *Ulmus* pollen probably reflects wind transport from distant sources. The bottom of zone A at Houghton Bog has been dated at 11,800 ± 730 B.P.
10. Mosses from an organic bed deposited 12,100 ± 400 years ago along the southern edge of Lake Iroquois near Lockport, N.Y., and a pollen spectrum from associated lacustrine sediments indicate the existence of a mosaic of plant communities in northwestern New York at this time. Species characteristic of dry dune sand, rich fens, and better drained fen edges probably occupied the area between the lake edge and a spruce-fir-larch forest occurring some distance inland. Exposed rocky habitats may have existed also. The occurrence of two typical arctic and subarctic mosses, *Aulacomnium acuminatum* and *A. turgidum,* indicates the possible presence of limited patches of tundra vegetation.
11. The spruce-pine woodland disappeared from 9500 to 10,500 years ago near the Valley Heads sites and was succeeded by zone B forests in which *Pinus*

Strobus held a dominant position. *Abies balsamea* flourished briefly during the transition. At some sites, lower pine-birch and upper pine-oak subzones can be distinguished. A *Pinus Strobus* cone was recovered from sediments about 10,500 years old at Protection Bog and clearly establishes the presence of this species in southwestern New York during the deterioration of the spruce-pine woodland. The B zone pine peak was dated at 9030 ± 150 B.P. at Protection Bog.

12. Zone C-1 is characterized by high percentages of *Tsuga canadensis* and increasing values for *Fagus grandifolia.* Other species which grow on the Allegheny Plateau at the present time are also represented in this zone. The similarity of the pollen assemblages near the end of zone C-1 and those found immediately beneath the presettlement/post-settlement boundary indicate that the zone records the regional development of forests of the hemlock-northern hardwoods type. Forest composition likely was as complex as now occurs in the upland. No major changes took place in the vegetation of southwestern New York during the duration of the C-1, although the *Fagus* increase may indicate a trend toward increased mesophytism.
13. An abrupt hemlock decline at Allenberg, Houghton, and Protection Bogs, which has been dated at 4390 ± 110 B.P. at the last named site, marks the beginning of zone C-2. The relative frequency of *Acer saccharum, Betula, Carya, Fagus, Fraxinus, Pinus Strobus, and Quercus* pollen show small increases in this zone. However, absolute pollen frequency data imply that these changes were induced by a decrease in the total number of hemlock grains being deposited per unit volume. Rather than a long interval of xeric, continental climate, the C-2 in southwestern New York seems to be a result of differences in hemlock abundance alone. Severe drought, which is known to cause heavy hemlock mortality in existing stands, occurring during several successive years or tens of years is postulated as the cause of the hemlock decline. Biotic factors, including man, may or may not have played a secondary role. Hemlock was never completely eliminated from southwestern New York during the C-2.
14. Subzone C-3a began 1270 ± 95 years ago at Protection Bog and records the return of hemlock to a position of prominence in the regional vegetation. This change may have been influenced by a climatic trend toward greater moisture during the past several millenia, but the hemlock return following the low early in C-2 time may represent successional recovery. There is some evidence that Indian agriculture is recorded in the upper half of this subzone.
15. European settlement and forest clearance occurred during the deposition of the topmost pollen assemblages belonging to subzone C-3b. Pollen from agricultural indicators, including *Fagopyrum, Zea,* and other cereals, was found in this subzone and the high frequencies of *Ambrosia,* Cheno-Am., *Plantago,* and *Rumex* pollen, species which grow in disturbed habitats, are characteristic. Subzone C-3b sediments contain large quantities of silt and clay blown in from bare areas around the basins.

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APPENDIX A

FOREST STAND DATA: TREES AND SAPLINGS, CANADAWAY CREEK GAME MANAGEMENT AREA,* CHAUTAUQUA COUNTY, NEW YORK

Species and Size Class	Relative Frequency	Relative Density	Relative Dominance	Importance Value	Absolute Density/Acre	Absolute Dominance/Acre
Acer saccharum						
Trees	58.5%	76.6%	80.1%	215.2	76.4	19,596.6
Saplings	60.0%	79.8%	70.6%	210.4	315.0	768.6
Fagus grandifolia						
Trees	22.0%	12.5%	16.4%	50.9	12.5	3,982.9
Saplings	18.6%	11.2%	11.9%	41.7	44.1	129.2
Tsuga canadensis						
Trees	17.1%	9.9%	3.4%	30.4	9.9	844.5
Saplings	8.6%	3.7%	8.0%	20.3	14.7	87.2
Prunus serotina						
Trees	1.2%	0.5%	0.1%	1.8	0.5	11.9
Magnolia acuminata						
Trees	1.2%	0.5%	0.1%	1.8	0.5	14.2
Fraxinus americana						
Saplings	5.7%	2.7%	5.4%	13.8	10.5	58.9
Betula alleghaniensis						
Saplings	4.3%	1.6%	3.0%	8.9	6.3	32.3
Ostrya virginiana						
Saplings	1.4%	0.5%	0.6%	2.5	2.1	6.6
Cornus alternifolia						
Saplings	1.4%	0.5%	0.6%	2.5	2.1	6.6

* New York State Department of Environmental Conservation.

APPENDIX B

FOREST STAND DATA: HERBS AND SEEDLINGS, CANADAWAY CREEK GAME MANAGEMENT AREA,* CHAUTAUQUA COUNTY, NEW YORK

Species and Size Class	Relative Frequency
Acer saccharum	
under 12 inches	24.2%
over 12 inches	9.2%
Arisaema triphyllum	18.3%
Viola incognita	9.2%
Fraxinus americana	
under 12 inches	6.5%
Dryopteris spinulosa var. *intermedia*	5.9%
Euonymus obovatus	5.9%
Dennstaedtia punctilobula	3.3%
Epifagus virginiana	2.6%
Phytolacca americana	2.6%
Aster divaricatus	1.9%
Viola canadensis	1.9%
Allium tricoccum	0.7%
Asarum canadensis	0.7%
Caulophyllum thalictroides	0.7%
Disporum lanuginosum	0.7%
Fagus grandifolia	
under 12 inches	0.7%
over 12 inches	1.9%
Galium sp.	0.7%
Hepatica acutiloba	0.7%
Monotropa uniflora	0.7%
Rhus radicans	0.7%
Viola rotundifolia	0.7%

* New York State Department of Environmental Conservation.

APPENDIX C

FOREST STAND DATA: TREES AND SAPLINGS, FORESTRY DEPARTMENT* PLANTATION #11, ERIE COUNTY, NEW YORK

Species and Size Class	Relative Frequency	Relative Density	Relative Dominance	Importance Value	Absolute Density/Acre	Absolute Dominance/Acre
Acer saccharum						
Trees	24.8%	24.0%	34.0%	82.8	66.9	11,694.1
Saplings	41.3%	49.2%	51.7%	142.2	63.0	264.6
Fagus grandifolia						
Trees	23.3%	26.0%	26.6%	75.9	72.5	9,113.3
Saplings	33.3%	26.2%	26.9%	86.4	33.6	137.8
Tsuga canadensis						
Trees	21.7%	24.5%	13.6%	59.8	68.3	4,671.7
Saplings	20.0%	21.3%	15.6%	56.9	27.3	79.2
Prunus serotina						
Trees	16.3%	16.1%	19.7%	52.1	44.9	6,735.0
Tilia americana						
Trees	6.2%	4.2%	2.3%	12.7	11.7	812.0
Saplings	2.7%	1.6%	2.9%	7.2	2.1	14.9
Ostrya virginiana						
Trees	2.3%	1.6%	0.9%	4.8	4.5	332.6
Fraxinus americana						
Trees	1.6%	1.0%	0.5%	3.1	2.8	149.5
Betula alleghaniensis						
Trees	1.6%	1.0%	0.3%	2.9	1.4	46.3
Saplings	2.7%	1.6%	2.9%	7.2	2.1	14.9
Juglans cinerea						
Trees	0.8%	0.5%	1.1%	2.4	1.4	376.3
Ulmus americana						
Trees	0.8%	0.5%	0.6%	1.9	1.4	215.5
Acer rubrum						
Trees	0.8%	0.5%	0.4%	1.7	1.4	121.3

* County of Erie.

APPENDIX D

FOREST STAND DATA: HERBS AND SEEDLINGS, FORESTRY DEPARTMENT* PLANTATION ♯11, ERIE COUNTY, NEW YORK

Species and Size Class	Relative Frequency	Species and Size Class	Relative Frequency	Species and Size Class	Relative Frequency
Acer saccharum		*Tilia americana*		*Athyrium Felix-femina*	0.4%
under 12 inches	15.7%	under 12 inches	2.0%	*A. thelypterioides*	0.4%
over 12 inches	8.9%	*Trillium grandiflorum*	2.0%	*Botrychium* sp.	0.4%
Prunus serotina		*Ostrya virginiana*		*Carex plantaginea*	0.4%
under 12 inches	11.7%	under 12 inches	1.6%	*Carya cordiformis*	
Acer rubrum		*Botrychium virginianum*	1.2%	under 12 inches	0.4%
under 12 inches	10.1%	*Polygonatum pubescens*	1.2%	*Dicentra* sp.	0.4%
over 12 inches	0.4%	*Actaea pachypoda*	0.8%	*Epipactis Helleborine*	0.4%
Fraxinus americana		*Carex* sp.	0.8%	*Hepatica acutiloba*	0.4%
under 12 inches	6.5%	*Caulophyllum thalictroides*	0.8%	*Hieracium* sp.	0.4%
Viola sp.	4.0%	*Circaea quadrisulcata*	0.8%	*Maianthemum canadense*	0.4%
V. incognita	3.2%	*Cornus alternifolia*	0.8%	*Mitella diphylla*	0.4%
Arisaema triphyllum	2.4%	*Epifagus virginiana*	0.8%	*Osmorhiza Claytoni*	0.4%
Geranium Robertianum	2.4%	*Impatiens* sp.	0.8%	*Oxalis montana*	0.4%
Ulmus americana		*Lycopodium complanatum*		*Phlox divaricata*	0.4%
under 12 inches	2.4%	var. *flabelliforme*	0.8%	*Podophyllum peltatum*	0.4%
Dentaria diphylla	2.0%	*Mitchella repens*	0.8%	*Polystichum acrostichoides*	0.4%
Dryopteris spinulosa		*Ribes* sp.	0.8%	*Tsuga canadensis*	
var. *intermedia*	2.0%	*Tiarella cordifolia*	0.8%	over 12 inches	0.4%
Fagus grandifolia		*Viola canadensis*	0.8%	*Veronica officinalis*	0.4%
under 12 inches	2.0%	*V. rotundifolia*	0.8%		
over 12 inches	0.4%				

* County of Erie.

APPENDIX E

FOREST STAND DATA: TREES AND SAPLINGS, ZOAR VALLEY PROPERTY ♯12,* ERIE COUNTY, NEW YORK

Species and Size class	Relative Frequency	Relative Density	Relative Dominance	Importance Value	Absolute Density/Acre	Absolute Dominance/Acre
Acer saccharum						
Trees	48.0%	68.2%	52.9%	169.1	78.9	13,789.4
Saplings	20.5%	22.2%	27.4%	70.1	33.6	131.7
Fagus grandifolia						
Trees	26.0%	16.2%	35.7%	77.9	18.7	9,313.7
Saplings	43.2%	51.4%	31.1%	125.7	77.7	149.2
Tsuga canadensis						
Trees	16.0%	10.4%	2.7%	29.1	12.0	692.3
Saplings	29.5%	22.2%	35.9%	87.6	33.6	172.3
Tilia americana						
Trees	4.0%	2.1%	3.2%	9.3	2.4	838.5
Fraxinus americana						
Trees	3.0%	1.6%	2.6%	7.2	1.9	699.5
Betula alleghaniensis						
Trees	1.0%	0.5%	0.1%	1.6	0.6	38.2
Ostrya virginiana						
Saplings	4.5%	2.8%	5.3%	12.6	4.2	25.3
Carpinus caroliniana						
Saplings	2.3%	1.4%	0.3%	4.0	2.1	1.6

* New York State Department of Environmental Conservation, Multiple Use Land, Acquisition ♯ Catt. 8.3.9.

APPENDIX F

FOREST STAND DATA: HERBS AND SEEDLINGS, ZOAR VALLEY PROPERTY #12,*
ERIE COUNTY, NEW YORK

Species and Size Class	Relative Frequency	Species and Size Class	Relative Frequency	Species and Size Class	Relative Frequency
Acer saccharum		*Athyrium thelypterioides*	1.1%	*Acer rubrum*	
under 12 inches	13.4%	*Carya cordiformis*		under 12 inches	0.4%
over 12 inches	12.4%	under 12 inches	0.7%	*Actaea* sp.	0.4%
Arisaema triphyllum	10.2%	over 12 inches	0.4%	*Adiantum pedatum*	0.4%
Fraxinus americana		*Dennstaedtia punctilobula*	1.1%	*Aster divaricatus*	0.4%
under 12 inches	9.2%	*Galium* sp.	1.1%	*A. lateriflorus*	0.4%
over 12 inches	2.1%	*Geranium Robertianum*	1.1%	*Athyrium Felix-femina*	0.4%
Fagus grandifolia		*Prunus serotina*		*Carex plantaginea*	0.4%
under 12 inches	2.5%	under 12 inches	0.4%	*C.* sp.	0.4%
over 12 inches	6.0%	over 12 inches	0.7%	*Circaea alpina*	0.4%
Viola incognita	4.9%	*Botrychium virginianum*	0.7%	*Eupatorium rugosum*	0.4%
Dryopteris spinulosa		*Cornus alternifolia*	0.7%	*Impatiens* sp.	0.4%
var. *intermedia*	3.9%	*Epipactis Helleborine*	0.7%	*Lycopodium lucidulum*	0.4%
Caulophyllum thalictroides	2.8%	*Monotropa uniflora*	0.7%	*Potentilla* sp.	0.4%
Hepatica acutiloba	2.8%	*Osmorhiza Claytoni*	0.7%	*Ribes* sp.	0.4%
Viola rotundifolia	2.5%	*Tilia americana*		*Sambucus canadensis*	0.4%
V. pensylvanica	2.5%	under 12 inches	0.7%	*Tiarella cordifolia*	0.4%
V. canadensis	2.1%	*Ulmus americana*		*Trillium erectum*	0.4%
Circaea quadrisulcata	1.4%	under 12 inches	0.7%	*T.* sp.	0.4%
Maianthemum canadense	1.4%	*Viola* sp.	0.7%	*Urtica procera*	0.4%
Actaea pachypoda	1.1%				

* New York State Department of Environmental Conservation, Multiple Use Land, Acquisition # Catt. 8.3.9.

APPENDIX G

POLLEN SPECTRA ABOVE AND BELOW GYTTJA SAMPLES USED FOR C-14 AGE DETERMINATION AT PROTECTION BOG

Taxa \ Depths (m)	3.56	3.66	5.35	5.45
Arboreal Pollen (AP)*				
Picea	——	——	0.7	——
Abies	——	——	0.6	0.4
Larix	——	——	0.3	——
Pinus undifferentiated	0.9	0.5	20.9	21.2
P. haploxylon	1.4	1.4	22.6	23.6
P. diploxylon	0.2	0.2	3.2	2.9
Juniperus	——	——	——	0.1
Tsuga	16.7	23.2	2.1	1.5
Fagus	35.4	38.2	0.7	0.3
Acer saccharum	8.6	7.7	1.5	1.3
Tilia	0.9	0.6	0.3	——
Fraxinus 4-colpate	3.9	1.8	0.6	0.6
Juglans cinerea	1.3	0.3	0.1	0.3
Carya	1.4	1.1	1.0	0.6
Quercus	6.8	7.5	22.3	19.5
Ulmus	5.0	6.4	6.0	6.0
Betula	11.0	5.4	6.2	8.8
Fraxinus 3-colpate	2.0	1.9	1.2	2.3
Acer rubrum	——	0.3	——	——
Carpinus-Ostrya	0.8	0.6	6.0	7.2
Corylus	——	——	0.4	0.7
Platanus	0.9	1.4	0.4	0.4
% AP	97.3	98.7	97.3	97.8

Taxa \ Depths (m)	3.56	3.66	5.35	5.45
Nonarboreal Pollen (NAP)*				
Alnus	0.6	0.3	0.7	0.5
Salix	0.3	——	0.7	0.1
Viburnum	0.3	——	——	——
Rosaceae	0.2	——	——	——
Cyperaceae	0.3	0.2	0.3	0.7
Gramineae	——	——	0.1	0.4
Ambrosia	0.3	0.2	0.1	——
Artemisia	0.2	0.2	0.3	0.1
Xanthium	0.3	——	——	0.1
High-spine Compositae	——	0.2	0.3	——
Cheno-Am.	0.2	——	——	——
Ranunculus	——	0.2	——	——
Thalictrum	——	0.2	——	——
% NAP	2.7	1.3	2.7	2.2
Misc. Pollen and Spores (MP)†				
Ericaceae	0.5	0.2	——	——
Nuphar	——	——	0.4	——
Sarracenia	0.2	0.2	——	——
Polypodiaceae	——	0.2	3.0	3.3
Osmundaceae	0.5	0.5	——	——
broken Abietineae	——	——	1.1	0.4
unfamiliar	——	——	0.1	——
unknown	2.7	4.0	3.4	1.7

* Percentage base: sum AP + NAP.
† Percentage base: sum AP + NAP + MP.

APPENDIX H

PERCENTAGES OF MINOR POLLEN AND SPORE TYPES NOT SHOWN ON POLLEN DIAGRAM: PROTECTION BOG

Depths (m) \ Taxa	*Ephedra*	*Juniperus*	*Liquidambar*	*Nyssa sylvatica*	*Cephalanthus*	*Myrica*	Rosaceae	*Viburnum*	Caryophyllaceae	*Coptis*	*Gentiana* comp.*	Labiatae	Leguminosae	*Polygonum*	*Potentilla palustris*	*Ranunculus*	Umbelliferae	Urticaceae	*Vitis*	*Xanthium*	*Myriophyllum*	*Sagittaria*	*Sarracenia*	*Sparganium*	*Utricularia*	Ophioglossaceae
0.000	—	0.1	0.1	—	—	—	0.3	0.1	—	—	—	—	—	—	—	0.1	0.2	0.1	0.2	—	—	0.1	—	—	—	—
0.025	—	—	—	—	—	—	0.7	—	—	—	—	—	0.1	—	—	0.1	0.2	—	—	—	—	0.3	—	—	—	—
0.075	—	—	0.1	—	—	—	0.2	0.2	—	—	—	—	—	—	—	0.1	0.2	—	—	—	—	—	0.1	—	—	—
0.125	—	—	0.1	—	—	—	0.4	—	0.1	—	—	—	0.6	—	—	—	—	—	—	—	—	0.2	0.1	—	—	—
0.175	—	—	0.1	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	—	—	0.2	—	—	—	—
0.225	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
0.275	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
0.325	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—
0.425	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—	—	—	—
0.575	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	—
0.725	—	—	—	—	—	—	—	—	—	0.5	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—
0.925	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.225	—	—	—	0.3	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.475	—	—	0.2	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.725	0.2	—	—	0.2	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.975	—	—	—	0.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—
2.225	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—
2.475	0.2	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—
2.725	—	—	—	0.3	—	—	—	0.2	—	—	—	0.2	—	—	0.2	—	—	—	—	—	—	—	0.2	—	—	0.2
2.975	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—
3.225	—	—	0.2	0.2	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	0.2	—	—	—
3.475	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	0.1
3.725	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3.975	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.3	—	—	—
4.225	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
4.475	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
4.725	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—
4.875	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—	—	—	—
5.025	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—
5.175	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5.325	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5.475	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5.625	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—
5.775	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	0.2	—	—
5.925	—	—	—	—	—	—	—	—	—	—	0.1	—	—	—	—	—	0.1	—	—	—	—	—	—	0.1	—	0.1
6.035	—	—	0.1	—	—	0.1	0.1	—	—	—	—	—	—	—	—	0.1	—	—	—	0.1	—	—	—	0.5	—	0.1
6.115	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	0.1	—	—	—	—	—	—	—	—	0.1
6.195	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	0.6	—	0.1
6.265	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—
6.325	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	0.1	0.1	—

* The notation "comp." after certain pollen taxa indicates the degree of certainty in the identification of difficult pollen grains (Benninghoff & Kapp, 1962). It is used when a grain is provisionally assigned to a taxon and to convey that uncertainty exists about the conclusiveness of identification. If no notation follows a taxon, the identification is considered positive.

APPENDIX I

PERCENTAGES OF MINOR POLLEN AND SPORE TYPES NOT SHOWN ON POLLEN DIAGRAM: HOUGHTON BOG — SECTION A

Depths (m) \ Taxa	*Cephalanthus*	*Rhamnus* comp.	*Rhus*	Rosaceae	*Sambucus*	*Viburnum*	Caryophyllaceae	*Coptis*	Labiatae	Leguminosae	*Ranunculus*	Rubiaceae	*Thalictrum*	Umbelliferae	*Sagittaria*	*Sparganium*	*Typha*	*Utricularia*	Ophioglossaceae
0.000	—	—	—	0.6	—	0.5	—	—	—	0.2	—	—	—	0.2	0.1	—	0.1	—	—
0.025	0.2	0.1	0.1	0.3	0.2	—	0.1	—	—	—	—	—	0.1	0.3	—	—	—	—	0.2
0.075	0.1	—	—	—	—	—	0.1	—	0.1	0.2	0.1	0.1	—	—	0.3	0.1	0.1	—	0.1
0.125	—	—	—	0.3	—	—	—	—	—	—	0.1	—	—	—	—	—	—	—	0.1
0.175	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
0.225	0.2	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
0.375	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—
0.725	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—
0.925	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—
1.225	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.425	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.725	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2
1.925	—	—	—	—	—	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	—
2.225	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—
2.475	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2.725	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—
2.975	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3.225	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3.425	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—
3.725	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—	—	—	—	—	—	—
3.925	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—

APPENDIX J

PERCENTAGES OF MINOR POLLEN AND SPORE TYPES NOT SHOWN ON POLLEN DIAGRAM: HOUGHTON BOG — SECTION B

Depths (m) \ Taxa	*Celtis*	*Liquidambar*	*Nyssa sylvatica*	Ericaceae	*Nemopanthus*	*Rhamnus* comp.	*Rosaceae*	Caryophyllaceae	*Coptis*	*Gentiana* comp.	*Impatiens* comp.	Rubiaceae	*Rumex*	*Thalictrum*	Umbelliferae	*Xanthium*	*Brasenia*	*Nuphar*	*Nymphaea*	*Menyanthes*	*Proserpinaca*	*Sagittaria*	*Sarracenia*	*Typha*	*Utricularia*
4.13	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	0.3	0.2	—	—	—	—	—	—
4.38	—	—	—	—	0.7	—	0.2	—	—	—	—	—	0.4	0.4	—	—	—	—	—	—	—	—	—	—	—
4.63	—	—	—	—	0.2	—	—	—	—	—	—	—	—	0.2	—	—	—	0.3	0.2	—	—	—	—	—	—
4.88	—	—	—	—	0.2	—	—	—	—	0.4	—	—	—	0.2	—	—	—	0.6	0.2	—	—	—	0.4	—	—
5.13	—	—	—	—	0.4	0.2	—	—	—	—	—	—	—	—	—	—	—	0.6	0.4	—	—	—	—	0.1	—
5.38	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	0.4	—	—	—	—	—	—	—
5.63	0.2	—	—	—	—	0.4	—	—	—	—	—	—	—	0.2	—	—	0.2	0.2	0.3	—	—	—	—	0.2	—
5.88	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—
6.13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6.38	0.2	—	—	—	0.2	—	0.2	—	—	—	0.2	0.2	—	0.2	—	—	—	0.3	—	—	—	—	—	—	—
6.63	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6.88	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	0.1	—	—	—	—	—	—	—
7.06	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7.21	—	0.2	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—
7.36	—	—	0.2	0.2	—	—	—	—	—	—	—	0.2	—	—	—	—	—	0.3	—	—	—	—	—	—	—
7.56	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
7.71	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	0.5	—	—	—	—	—	—	—
7.86	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8.01	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8.13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	0.2	—	—	—	—	—	—	—
8.25	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
8.37	0.2	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8.49	0.2	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8.61	0.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8.73	—	—	0.2	0.2	—	—	—	—	—	—	—	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	0.2
8.84	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2
8.96	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—
9.01	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.3
9.07	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—
9.13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9.19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9.25	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9.31	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	0.5	0.2	—	—	—	—	—	—	0.3	—	—	—
9.41	—	—	—	0.2	—	—	—	—	—	—	—	—	0.2	0.5	—	—	—	—	—	—	—	—	—	—	—
9.55	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9.67	—	—	—	—	—	—	—	0.2	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	0.2	—
9.79	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	0.3	0.3	—	0.2	—
9.91	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

APPENDIX K

PERCENTAGES OF MINOR POLLEN AND SPORE TYPES NOT SHOWN ON POLLEN DIAGRAM: ALLENBERG BOG — SECTION A

Depths (m) \ Taxa	*Juglans nigra*	*Liquidambar*	*Magnolia acuminata*	*Cephalanthus*	*Myrica*	Rosaceae	*Viburnum*	Caryophyllaceae	*Coptis*	Labiatae	Leguminosae	*Ranunculus*	*Thalictrum*	Umbelliferae	Urticaceae	*Vitis*	*Xanthium*	*Sagittaria*	*Sarracenia*	*Sparganium*	*Utricularia*	*Equisetum*	Ophioglossaceae
0.000	0.2	0.1	—	—	—	2.6	0.1	—	—	—	—	—	—	—	0.1	—	0.1	—	—	—	—	—	—
0.025	—	—	—	0.1	—	1.1	0.3	—	—	0.3	0.2	—	—	0.5	—	0.2	0.1	0.3	—	0.1	—	—	0.1
0.075	0.2	0.1	—	—	—	0.7	0.3	—	—	—	0.2	—	—	0.2	0.2	—	0.1	—	—	0.1	—	—	—
0.125	0.2	0.1	—	0.1	0.1	1.1	2.3	—	—	0.1	0.1	0.4	—	—	—	—	—	0.1	0.1	—	—	0.1	—
0.175	0.3	0.2	—	—	—	0.3	1.2	—	—	—	—	—	—	—	0.2	—	—	—	0.1	—	—	—	—
0.225	0.2	—	0.3	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	0.4	—	—	—	—
0.275	—	0.2	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	1.6	—	—	—	—
0.325	—	0.2	—	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—	—	—	0.7	—	—	—	—
0.375	0.3	—	0.2	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	0.5	—	—	—	—
0.425	0.2	—	—	—	—	0.2	0.2	—	—	—	—	—	0.3	—	—	—	—	—	0.4	—	—	—	—
0.475	0.2	—	—	—	0.2	—	0.5	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—
0.675	—	—	—	—	—	0.2	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—
0.925	—	—	—	—	—	—	0.9	—	0.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.117	—	—	—	—	—	0.3	0.2	—	0.3	—	—	—	0.2	—	—	—	—	—	0.7	—	—	—	—
1.425	—	—	0.2	—	—	—	0.2	—	—	—	—	—	0.2	—	—	—	—	—	0.3	—	—	—	—
1.675	0.2	—	—	—	—	1.1	0.5	—	0.2	—	—	—	0.2	—	—	—	—	—	0.4	—	—	—	—
1.925	—	0.2	—	—	—	—	—	0.2	—	—	—	—	—	—	0.3	—	—	—	0.2	—	0.2	—	—
2.175	0.2	—	—	—	—	0.3	0.5	—	—	—	—	—	0.5	—	—	—	—	—	0.3	—	0.1	0.1	—
2.425	—	—	—	—	—	0.5	0.3	—	—	—	—	—	0.2	—	—	—	—	—	0.1	—	0.1	—	—
2.675	—	—	—	—	0.2	0.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2.925	0.2	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	0.3	—	—	—	—

APPENDIX L

PERCENTAGES OF MINOR POLLEN AND SPORE TYPES NOT SHOWN ON POLLEN DIAGRAM: ALLENBERG BOG — SECTION B

Depths (m) \ Taxa	*Juglans nigra*	*Liquidambar*	*Magnolia acuminata*	*Nyssa sylvatica*	*Cephalanthus*	*Myrica*	*Rhus*	Rosaceae	*Viburnum*	Caryophyllaceae	*Coptis*	*Epilobium*	Cichorioideae	Umbelliferae	Urticaceae	*Xanthium*	*Myriophyllum*	*Potamogeton*	*Sarracenia*	*Utricularia*	*Equisetum*	Ophioglossaceae
4.525	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
4.675	0.2	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	0.2	—	—	0.2	—	—	—
4.925	—	0.2	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	0.6	—	—	—
5.175	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.3	—	—	—
5.425	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.4	—	—	—
5.675	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—
5.925	—	0.2	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—
6.175	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6.425	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—	—
6.675	0.3	—	0.2	—	0.2	—	—	—	—	—	—	—	0.2	—	—	—	—	—	0.2	—	—	—
6.925	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	0.1	0.1	0.1	—
7.175	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—
7.425	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	—	—
7.675	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—
7.925	0.2	0.2	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	4.1	—	—	—	—
8.175	—	—	—	—	—	—	—	0.1	—	—	0.1	—	—	—	—	0.1	—	0.1	—	—	—	—
8.425	—	0.3	—	—	—	—	—	0.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8.675	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—
8.925	0.2	—	—	—	—	—	—	—	0.2	—	0.3	—	—	—	—	—	—	—	—	—	—	—
9.175	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9.425	0.3	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9.675	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9.925	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
10.175	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	0.1	—	—	—
10.425	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
10.675	—	—	—	0.2	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—
10.925	—	—	—	—	—	0.2	—	—	0.3	—	—	—	—	—	—	—	—	—	—	—	—	—
11.175	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—
11.425	—	0.2	—	—	—	—	—	—	0.2	—	—	—	—	—	0.2	—	—	—	—	—	—	0.2
11.675	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	0.2	0.2	—	—	0.2	—	—	—
11.925	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—
12.175	—	—	—	—	—	0.2	—	—	—	—	—	0.2	—	0.2	0.2	—	0.1	—	—	0.1	—	—
12.425	—	—	—	—	—	—	—	—	—	0.2	0.2	—	—	—	—	—	—	0.2	—	—	—	—

APPENDIX M

PERCENTAGES OF MINOR POLLEN AND SPORE TYPES NOT SHOWN ON POLLEN DIAGRAM: ALLENBERG BOG — SECTION C

Depths (m) \ Taxa	*Nyssa sylvatica*	*Rhus* comp.	Rosaceae	*Viburnum*	Caryophyllaceae	*Coptis*	*Epilobium*	*Galium* comp.	*Gentiana* comp.	Labiatae	*Polygonum*	*Ranunculus*	Umbelliferae	Urticaceae	*Xanthium*	*Eriocaulon*	*Menyanthes*	*Sagittaria*	*Sparganium*	*Isoëtes*	Ophioglossaceae	*Selaginella selaginoides*
11.525	—	—	—	—	—	—	—	—	—	—	—	—	—	0.3	—	—	—	—	—	—	—	—
11.675	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
11.875	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12.025	—	—	—	0.3	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—
12.175	—	—	0.4	—	—	—	—	—	—	—	—	—	—	0.4	—	—	—	—	—	—	—	—
12.325	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12.425	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12.625	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12.775	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	0.3	0.3	—	—	—
12.925	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	0.1	—
13.075	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	0.3	0.1	—	—	—
13.225	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	0.1	0.1	0.3	—	0.1	—
13.375	—	—	0.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.7	—	—	—
13.525	—	—	0.3	—	—	—	—	—	—	—	—	—	—	0.1	0.1	—	—	—	0.3	—	0.1	—
13.675	—	—	0.1	—	—	—	—	—	—	—	—	0.3	—	—	—	—	—	—	—	—	0.3	—
13.825	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	0.5	—	—	—
13.925	—	—	0.1	—	—	—	—	0.1	—	0.1	—	—	—	—	—	—	—	—	—	—	0.1	—
14.125	—	—	0.2	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	0.5	0.1	—	—
14.275	—	0.1	—	—	—	—	—	0.1	—	—	—	—	0.1	—	—	—	0.1	—	—	—	0.1	—
14.425	—	—	0.1	—	—	—	—	—	—	—	—	0.3	—	—	0.1	—	—	0.1	0.4	—	0.3	—
14.540	0.1	—	0.3	—	—	—	—	—	—	0.3	—	0.1	—	—	—	—	—	—	0.4	—	0.1	—
14.660	—	—	—	—	—	—	—	—	—	—	—	0.3	—	0.3	—	—	—	0.1	0.1	—	—	—
14.750	—	—	—	—	—	—	—	—	—	—	—	0.2	—	0.3	—	—	—	0.1	0.1	—	—	—
14.870	—	—	—	—	—	—	—	—	—	0.1	—	0.1	—	0.3	—	—	—	—	—	—	—	—
14.985	—	—	0.3	—	0.1	—	—	—	0.3	—	—	0.4	0.3	—	—	—	—	—	—	—	0.3	0.1
15.085	—	—	0.2	—	0.4	—	—	—	—	0.1	—	0.1	—	—	—	—	—	—	—	—	—	0.1
15.165	—	—	—	—	0.1	—	—	—	—	0.1	0.1	0.2	—	—	—	0.1	—	—	—	—	—	—

APPENDIX N

PERCENTAGES OF MINOR POLLEN AND SPORE TYPES NOT SHOWN ON POLLEN DIAGRAM: GENESEE VALLEY PEAT WORKS

Depths (m) \ Taxa	*Juglans nigra*	*Larix*	*Liquidambar*	*Nyssa sylvatica*	*Populus*	*Cephalanthus*	*Nemopanthus*	*Rhus* comp.	*Sambucus*	*Viburnum*	*Arceuthobium*	*Campanula rotundifolia*	*Coptis*	*Cornus canadensis*	*Dryas* comp.	*Empetrum* comp.	*Gentiana* comp.	Labiatae	*Lysimachia* comp.	*Polemonium* comp.	*Ranunculus*	*Saxifraga* comp.	Urticaceae	*Menyanthes*	*Myriophyllum*	*Proserpinaca*	*Sarracenia*	*Scheuchzeria*	*Typha*	*Utricularia*	Ophioglossaceae	unfamiliar spore type A
0.51	—	—	0.2	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
0.67	—	—	—	0.1	0.3	—	1.5	2.8	0.3	5.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.4	—	—	—	—	—
0.85	0.2	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	0.2	—	—	—
1.03	—	0.1	0.4	—	0.4	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.22	—	—	—	0.2	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.41	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.57	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.86	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2.14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	—	—	—
2.43	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2.69	—	—	—	—	0.7	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	0.2	—	—	—	—	—	—	—	—
2.94	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	—
3.19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—
3.45	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—
3.69	—	—	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	0.1	0.6	—	0.1	—	—	—	—	—	—	—	—	0.1	—	0.1	—
3.89	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.4	—	0.1	—	—	—	—	—	—	—	—	—	—	0.6	—	—
4.09	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.3	—	—
4.30	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	0.1	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—
4.50	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	—	—	—	0.1	—	—	—	—	—	—	—	0.1	—	—	—	0.1	0.1	—
4.60	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.3	—	—	—	0.3	0.1	—	—	—	0.1	—	—	—	—	—	—
4.70	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	0.1	—	—	—	—	0.6	—	0.3	—	—	—	—	0.1	—	—	0.3	0.4
4.74	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	—	—	—	—	—	0.3	—	—	—	—	—	—	—	0.4	0.2
4.80	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	—	0.5	—	0.1	—	0.2	—	—	—	—	0.1	0.4	0.6

Pollen Diagrams

1. Percentages of all pollen taxa on the left side of the sums column were computed using the sum of the arboreal and nonarboreal pollen excluding aquatics and pteridophytes.
2. Only major pollen taxa are included in the following diagrams. See Appendices H to N for a listing of minor types.
3. When a given pollen type occurs with regularity across some interval, but elsewhere is represented by only one or two grains, which may be stratigraphically isolated from other occurrences immediately above and below, a + symbol is used.

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